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Speciation in *Heliconius* (Lep., Nymphalidae): Morphology and Geographic Distribution[1,2]

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(Maps 1-30; Text-figures 1-173)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research under the late Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B. W. I." by William Beebe, *Zoologica,* 1952, Vol. 37, No. 13, pp. 157-184].

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I. Introduction

BATES' views on mimicry are now well known but it is not so widely appreciated that it was his observations on members of the genus *Heliconius* in the Amazon basin that really stimulated his curiosity. The diversity of this neotropical genus, both in speciation and intraspecific multiformity, has challenged taxonomists throughout the hundred years or so that material has been accumulated, but the principal difficulties that have faced museum workers are still pertinent. These include the shortage of reasonably long series of specimens from reliable localities and the relatively small number of localities from which collections have been obtained. Moreover, much of the older material is accompanied only by vague or erroneous locality data, but this is a point which has already been elaborated in the detailed study of *Heliconius melpomene* and *H. erato* (Emsley, 1964).

The taxonomic works of importance concerning *Heliconius* are those of Stichel & Riffarth (1905) and Seitz (1913), who used only macroscopic alary characters, and the more rational approach of Eltringham (1916), who employed also male genital characters in a determined effort to reduce the total number of recognized species. With the exception of Michener (1942), who introduced venation in a short revision of the subfamily, the only use of other morphological features is by Emsley (1963), who based a systematic arrangement of the subfamily on the shape and distribution of the androconia, the presence and shape of the signa on the bursa copulatrix, the shape of the female abdominal processes, the breadth of the duct to the spermathecal diverticulum, the proportionate lengths of the two components of the bifid pretarsal paronychia together with the structure of the male genital valves. These characters have also been found to be of relevance to the systematics of *Heliconius* and are the principal structures upon which this reassessment is based.

II. Acknowledgments, Materials and Methods

The materials upon which this study has been made are the collections of the British Museum (Natural History) at London and Tring, those of the Hope Department of Entomology at Oxford and the American Museum of Natural History in New York, and a portion of the collection of the Museum of Natural History in Paris. The author is indebted to the trustees of these institutions for study facilities and loan of specimens and particularly to Mr. Howarth and Mr. Tite of the British Museum at London and Tring respectively for their willing cooperation. Thanks are offered to Dr. E. W. Schmidt-Mumm[3] for a substantial gift of *Heliconius* specimens from his most useful Colombian collection and for his advice and assistance while the author was traveling in Colombia. Malcolm Barcant[4] must also be included in the acknowledgments for his assistance on field trips and for access to his comprehensive collection of Trinidad butterflies. The author is most grateful to Jocelyn Crane, Director of the New York Zoological Society's Department of Tropical Research, for the first instilling interest in this group and for her continued support, to Julie Emsley for her diligent assistance in the museums and for the drawings accompanying this text and to the National Science Foundation for the award of a grant (G-21071) which financed this work. Lastly, mention must be made of F. Martin Brown[5] who has kindly advised on this paper, which concerns a group in which he has been interested and most knowledgeable for many years.

The relevant parts of the dried museum material were removed, macerated in 5% potassium hydroxide and examined in glycerine. Structures dissected off museum specimens were preserved in glycerine in minute vials which were then attached by their stoppers to the pins of the specimens. No permanent slide preparations were made. The distribution of androconia was

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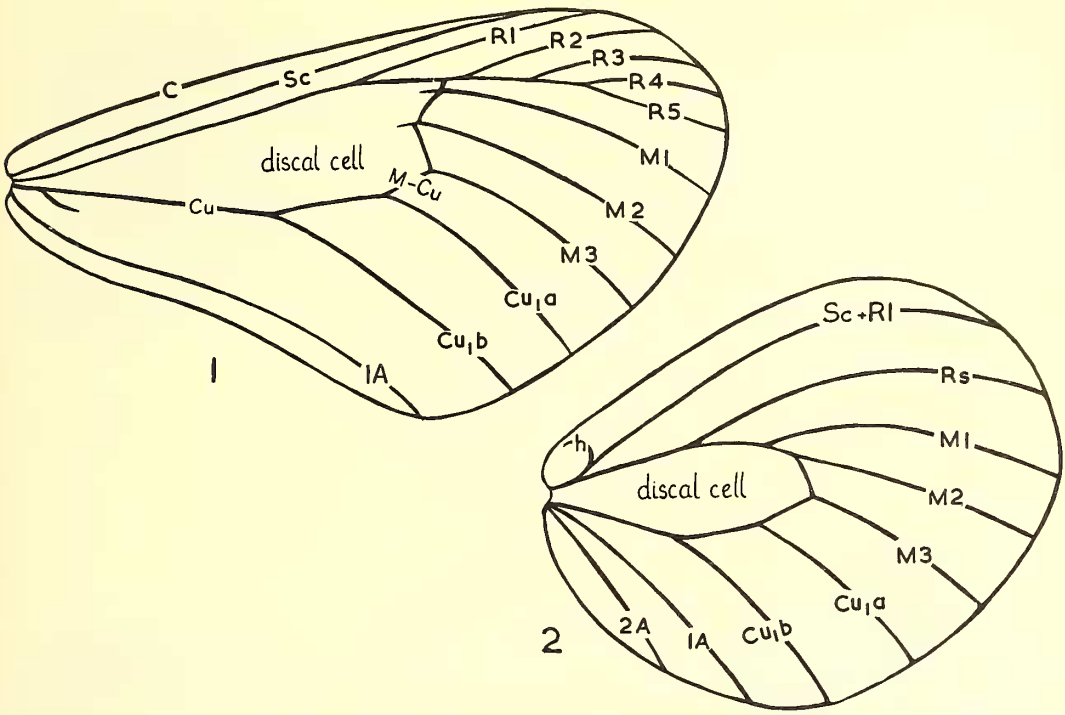


TEXT-FIGS. 1 & 2. Fore **(1)** and hind **(2)** wings of typical *Heliconius* to illustrate venational nomenclature. **C**—costa; **Sc**—subcosta; **R1** to **R5**—first to fifth branches of the radius; **Rs**—radial sector; **M1** to **M3**—first to third branches of the media; **Cu**—cubitus; **Cu1a** and **Cu1b**—branches of first cubitus; **1A** and **2A**—first and second anal veins; **H**—humeral branch of subcosta; **M-Cu**—medio-cubitus crossvein.

determined by microscopic examination of the wings while they were immersed in 90% alcohol. The reluctance of earlier lepidopterists to "damage" their specimens by such dissection has retarded the growth of our understanding of the systematics of *Heliconius* and probably of many other papilionoid groups.

In principal this paper is to be regarded as a study in evolutionary taxonomy and no special effort has been made to check the nomenclatorial precedence of the names used, or to become too deeply involved in the detailed variations within the species. The prime objective has been to define the geographic and polychromatic forms within species and to relate them to each other in such a way that their evolutionary history may be postulated.

III. Constitution and Geographic Distribution of *Heliconius*

Though the names used here are those adopted by Neustetter (1929), it has been possible to reduce the number of recognized species from 107 to 46. No new names are being proposed to associate the species as there is already a confusing number of infrageneric group names. Instead, species-groups will be suggested and the species held to be the most primitive in each association will be selected as the titular species of the group.

In order to facilitate the description of alary characters, the venational terminology is illustrated in Text-figs. 1 and 2, and the appearance of the major and minor elements of the color pattern can be identified by reference to Text-figs. 3-12 (and see Emsley, 1964, color plate I, figs. 1-8).

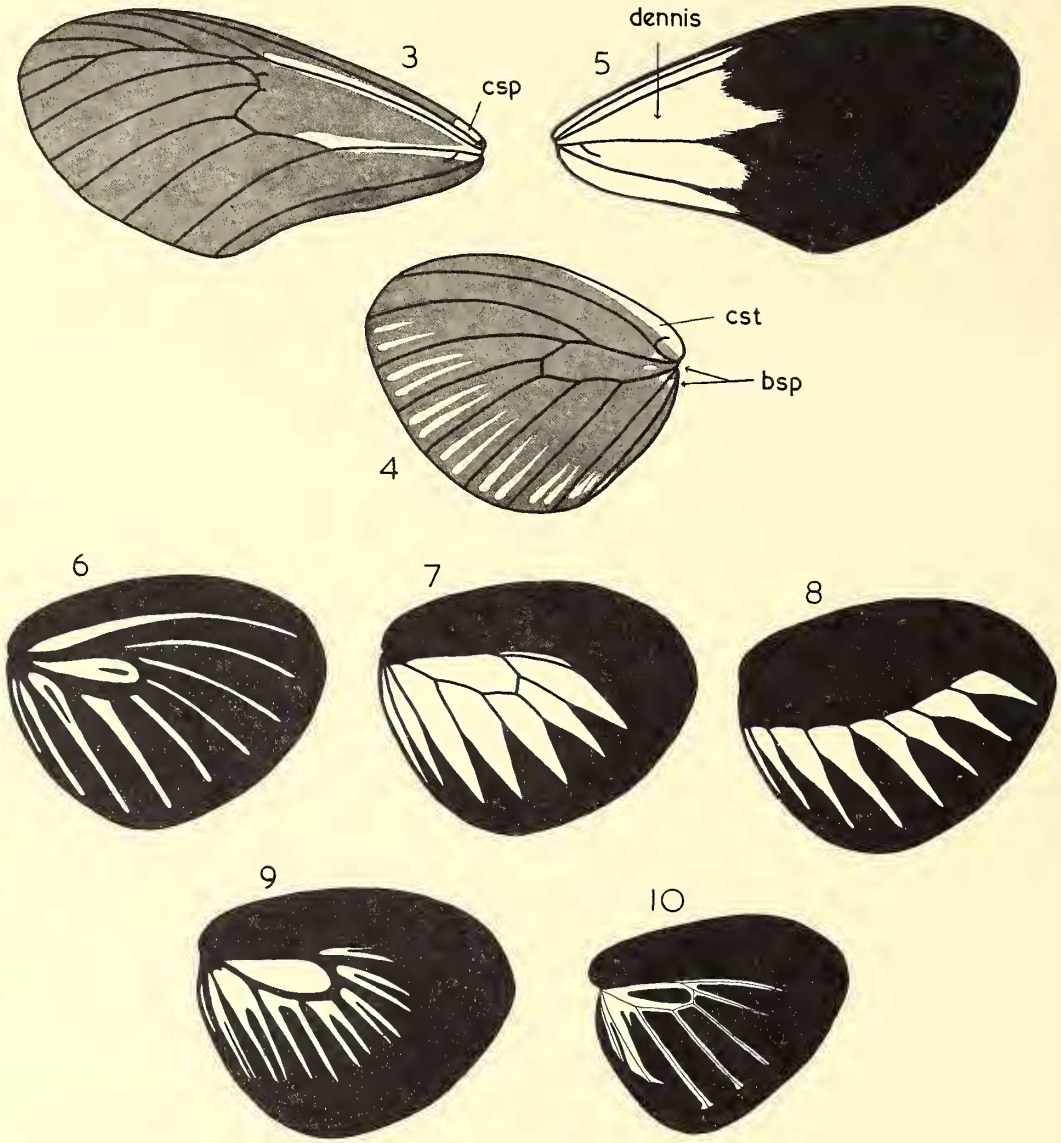
The nomenclatorial authorities are quoted:—"Author year: page" and the strictly taxonomic references are placed near the end of Section III so they do not mask the more interesting general references at the end of the paper.

Heliconiinae Swainson 1827: 187

Definition: Nymphalid Papilionoidea with the humeral branch of the subcosta at the anterior base of the hindwing recurrent and unforked (Text-fig. 2); the presence in males of androconia on some of the fore and/or hindwing veins and with a pair of lateral capitate processes developed from the posterior margin of the eighth abdominal segment of females.

Included genera and species are:

Philaethria Billberg 1820:77



TEXT-FIGS. 3-10. The elements of the color pattern of *Heliconius*. **3**, ventral view of right forewing to show costal spot (csp) and lines over radius and cubitus; **4**, similar view of hindwing to show costal streak (cst), basal spots (bsp) and paired intervenal white streaks; **5**, dorsal view of right forewing to show red base (= dennis); **6**, dorsal view of right hindwing to show ray in *H. erato;* **7**, ditto in *H. doris eratonius;* **8**, ditto in *H. melpomene timaretus;* **9**, ditto in *doris doris;* **10**, ditto in *H. tales*. About twice natural size.

P. dido (Clerk 1764, pl. 30)

Dryadula Michener 1942:4
D. phaetusa (Linnaeus 1758:478)

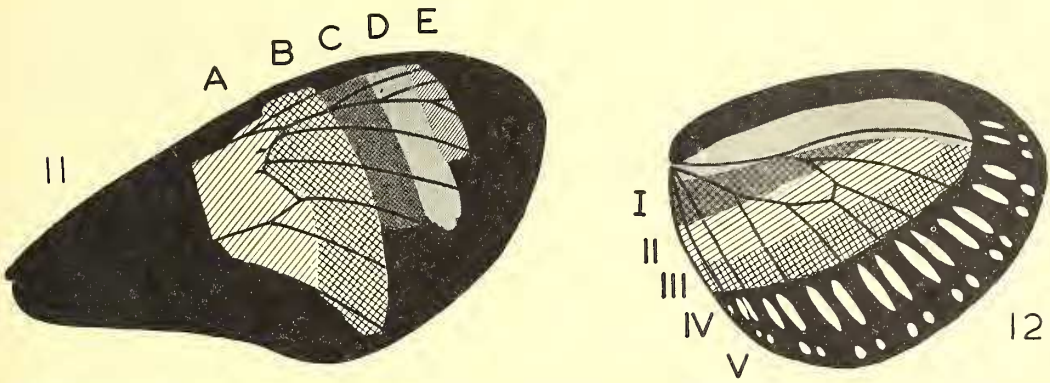
Agraulis Boisduval & Le Conte 1836:142
A. vanillae (Linnaeus 1758:482)

Dione Hübner 1818:31
D. juno (Cramer 1779:38)
D. moneta Hübner 1825, pl. 20.
D. glycera (C. & R. Felder 1861:102)

Podotricha Michener 1942:3
P. euchroia (Doubleday 1847:149)
P. telesiphe (Hewitson 1867b: 564)

Colaenis Hübner 1819:32 (see footnote 6)

[6]Since the survey of the subfamily (Emsley, 1963), it has been noticed that the Commission on Zoological Nomenclature rejected the generic name *Dryas* Hübner 1806 (opinion 278 on January 22, 1954, published October 1, 1954) on the grounds that it was included in a work which is inacceptable for nomenclatorial purposes (in tentamen).



TEXT-FIGS. 11 & 12. Diagrammatic representations of the positions of the forewing band (**11**) and hindwing bar (**12**) which are of common occurrence in *Heliconius*.

C. iulia (Fabricius 1775:509)

Heliconius Kluk 1802:82

46 species, discussed below.

Heliconius Kluk 1802:82 (see footnote 7)

Genotype: *Papilio charitonia* Linnaeus 1767:757

Designated by Hemming, 1933:223

Definition: Heliconiinae with the discal cell of the hindwing closed by cross-vein M2-M3 (Text-fig. 2).

Subgenus *Eueides* Hübner 1816:11

Subgenotype: *Nerëis dianasa* Hübner 1816:11

Definition: *Heliconius* with a narrow duct leading from the spermathecal diverticulum (Text-fig. 18) and four-segmented tarsi on the female foreleg (Text-figs. 14, 15). These characters are reinforced in most species by the acute angle through which the signa of the bursa copulatrix are curved and their tendency to asymmetry (Text-figs. 24, 25), and the exclusion of the androconia from the membrane around the hindwing veins Sc + R1 or Rs (Text-fig. 29).

THE *ALIPHERUS* GROUP

Group characters are the presence of androconia on hindwing veins Sc + R1, Rs, M1, M2, M3, Cu 1a and Cu 1b (Text-fig. 75), but only on forewing vein 1A; the strongly acute-angled and asymmetrical signa (Text-figs. 24, 25); the almost straight female processes (Text-fig. 161); and the coarsely spinose and unequal paronychial processes (Text-fig. 23).

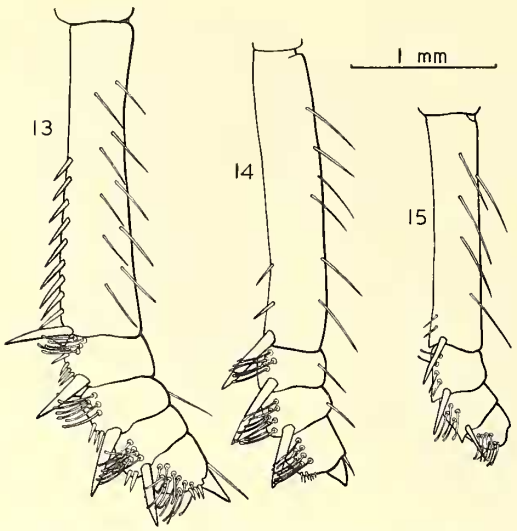
1. *Heliconius alipherus* (Godart 1819:246)

Map 1: Text-figs. 15, 23, 24, 25, 32, 75 and 161

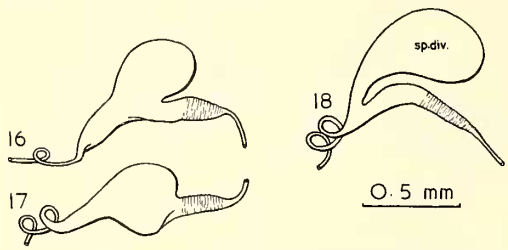
H. alipherus is the most widely distributed and stable species of *Heliconius*, extending from Mexico to upper Paraguay. It occurs on Trinidad and Tobago (and possibly Grenada) where as elsewhere within its range it is common. It is a small orange butterfly (wingspan ♂ 56 mm., ♀ 63 mm.) with a dorsal brown border which extends proximally as a series of weakly developed venal and intervenal spikes; there is also a dark line on the forewing along the discal border of R which curves posteriorly across M3, and another along 1A. The dark pattern of females is less strongly developed and the ground color is a little lighter. Ventrally the ground color has a pinkish tinge, the veins are brown and there are ochreous patches at the apex of the discal cell and at the distal extremity of the forewing. There are no red basal spots (Text-fig. 4) but the forewing costal spot (Text-fig. 3) and hindwing costal streak (Text-fig. 4) are differentiated in a darker orange.

The only appreciable geographic variation is a cline of increase in the intensity and extent of the dark markings and richness of the orange ground color from west of Colombia into South America east of the Andes. The pale and less maculate western and northern forms have been called *cillenulus* Seitz 1913:399 when the ground color is buff and *gracilis* Stichel 1903:23 when it is orange; they match the pale sympatric *Colaenis iulia moderata* Stichel 1907:12 which similarly occurs in Central America, and Colombia and Ecuador west of the Andes. The factor which contributes most to the pale appearance is the reduction, sometimes to total absence, of the dark forewing lines across M3 and along 1A.

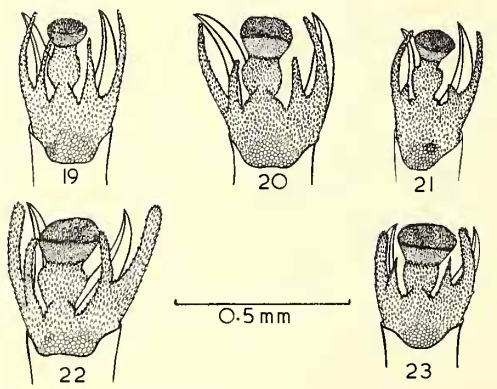
[7]Accepted as a valid generic name by the Commission on Zoological Nomenclature (opinion 382 of April 15, 1955, published January 24, 1956). Paclt, 1955: 431, gives evidence that Kluk's publication date was 1780.



TEXT-FIGS. 13-15. External view of right tarsi of female foreleg of **13,** *H. (Heliconius) melpomene;* **14,** *H. (Eueides) isabellae;* **15,** *H. (Eueides) alipherus.*



TEXT-FIGS. 16-18. Lateral view of spermatheca, with diverticulum (sp. div.), of **16,** typical member of subgenus *Heliconius;* **17,** *godmani* group of subgenus *Heliconius;* **18,** typical member of subgenus *Eueides.*



TEXT-FIGS. 19-23. Ventral view of meso or metapretarsus of **19,** *H. melpomene;* **20,** *H. wallacei;* **21,** *H. erato;* **22,** *H. isabellae;* **23,** *H. alipherus.*

Specific Characters: In addition to the group characters, there is the shape of the male genital valves (Text-fig. 32) and the absence of a spine at the apex of the female protarsus (Text-fig. 15).

THE *EDIAS* GROUP

Group features are the presence of androconia on many forewing veins (Text-fig. 98), on hindwing vein Sc + R1 and extensively on Rs (Text-fig. 76); the strongly curved female processes (Text-fig. 170); and the rotund signa (Text-fig. 149).

2. *Heliconius edias* Hewitson 1861:155

Map 2; Text-figs. 34, 76, 98, 149, 170

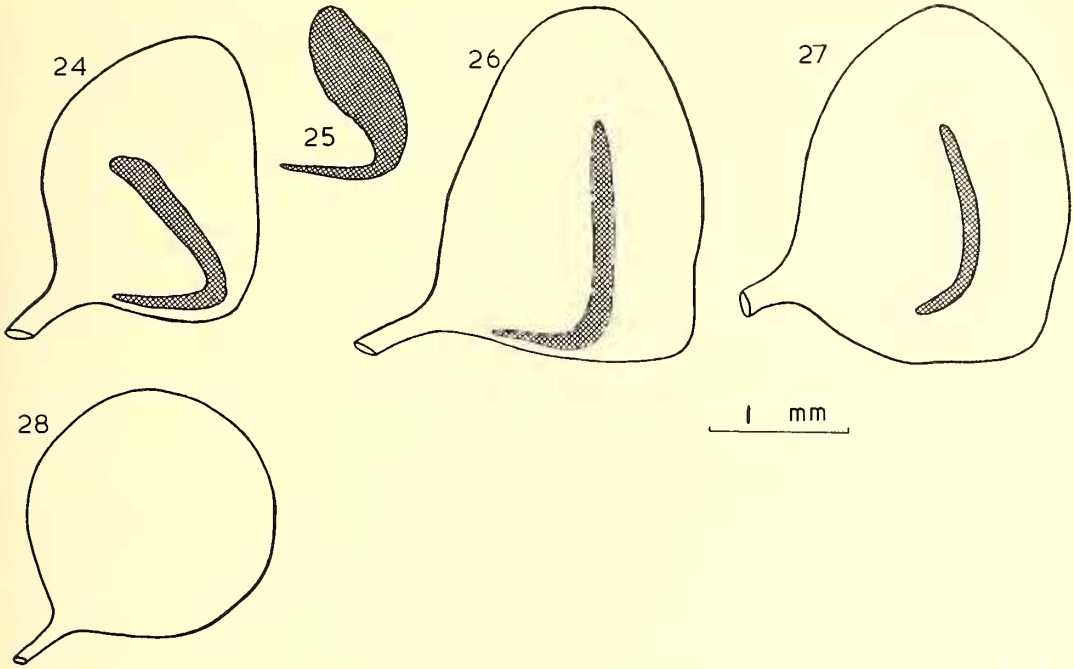
This species, though broadly restricted to the northern Andes, is differentiated into the western *eurysaces* Hewitson 1864:248, northern *vulgiformis* Butler & Druce 1872:102, and central *edias* and *umbratilis* Röber 1927:403. The wingspan approximates to 72 mm.

Though occurring in Costa Rica and perhaps as far north as Mexico, *vulgiformis* is the characteristic form from Panama and has three cream forewing spots in position A, one spot in position B and an interrupted band in position C (Text-fig. 11); there is no line over the cubitus but the post 1A margin is orange, and the hindwing has a broad orange bar in coalesced positions I + II + III + IV (Text-fig. 12). The forewing costal spot is orange and there may be a yellow spot enclosed by the recurrent branch of the hindwing subcosta (Text-fig. 4). There is a submarginal (position V) row of paired white spots on the ventral surface of the hindwing. Females are only slightly more pale than males.

The appearance of *edias,* from around the spurs of the Andes in northern Colombia, is similar to that of *vulgiformis* but the forewing band spots are larger and more orange, there is an orange line over the stem of the cubitus, and the peripheral black invades the distal hindwing vein endings. Females are much more pale than males.

To the west, on the Pacific slopes of Ecuador, the pale and diaphanous form *eurysaces* is quite distinct. The markings are vague with the pale orange line over the forewing cubitus broad and contiguous with the inner forewing band in position A, and the outer band in position C is very faint. The orange forewing costal spot is barely detectable. Females are even more pale than the males, which are not unlike the most pale female *edias.*

The status of *proculus* Doubleday 1848:146 and *luminosus* Stichel 1903:16 from the moun-

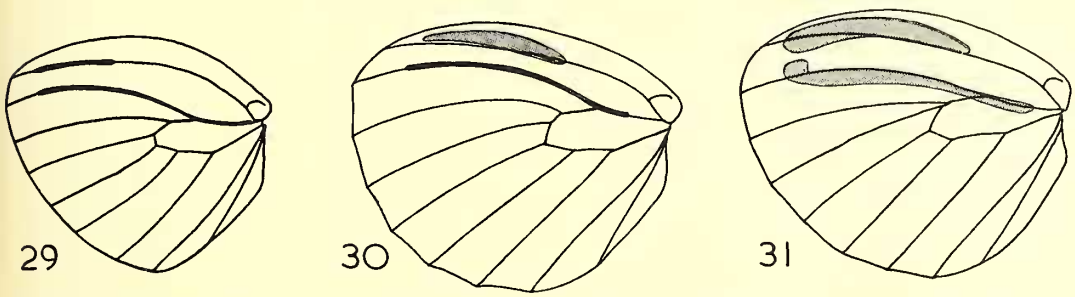


TEXT-FIGS. 24-28. Right lateral views of bursa copulatrices to show shape and orientation of signa. **24,** *H. alipherus;* **25,** right side of left signum of *H. alipherus* to demonstrate asymmetry; **26,** *H. melpomene* or *cydno* or *pachinus* or *ethillus* or *numatus* or *hecale* or *aristionus;* **27,** *H. doris;* **28,** *H. erato* and other non-signate species.

tains of Venezuela and eastern Colombia respectively is still uncertain, for they differ from *H. edias* in not having androconia on any forewing veins other that 1A, but the hindwing distribution is similar and more extensive than in *H. vibilius*. The female abdominal processes are strongly curved as in *H. edias* (Text.-fig. 170), and the male genital valves are of the long-processed *H. edias* type (Text-fig. 34), as are the signa (Text-fig. 149). The forewing band is only represented by a compact cream band in position A, which is a component of both *H. edias* and *H. vibilius,* and the forewing costal spot, which is orange in *H. edias* and yellow in *H. vibilius,* is orange and yellow in *proculus.* Temporarily, *proculus* is assigned to *H. edias* and is considered an isolated form in which the forewing androconia have been lost from all veins except 1A, but the position is unsatisfactory.

The form *ascidius* Schaus 1921:108 has not been seen.

SPECIFIC CHARACTERS: The presence of androconia on many forewing veins (Text-fig. 98) together with the shape of the male genital valves (Text.-fig. 34). The forms *luminosus* and *pro-*



TEXT-FIGS. 29-31. Dorsal views of left hindwings of male *Heliconius* to show the androconial distribution in **29,** *H. (Eueides) vibilius lampeto;* **30,** *H. (Heliconius) sapho congener;* **31,** *H. (Heliconius) pachinus.*

culus have forewing androconia only on 1A. Note that the genitalia alone are hard to distinguish from some members of the *vibilius* group.

THE *VIBILIUS* GROUP

Group features are the hindwing androconia only on veins Sc + R1 and Rs (Text-figs. 29, 76); the absence of androconia on all forewing veins, including 1A; the female abdominal processes which are similar to those of *H. alipherus* (Text-fig. 161); the strongly arched slightly asymmetrical signa (Text-fig. 150); and the development of a recurved hook at the dorsal base of the ventral component of the male genital valves (Text-figs. 33, 35, 36, 37) (a character which is shared with *H. edias*).

3. *Heliconius vibilius* (Godart 1819:245)

Map 3: Text-figs. 29, 33, 76, 150, 161

This is a wide-ranging species which extends from southern Brazil to eastern Colombia and from Panama to Guatemala and over which there is still some taxonomic uncertainty. The basic pattern is a dark brown ground color on which the forewing carries a pair of cream or orange bands in positions A and C, an orange line over the cubitus and an orange posterior border; on the hindwing there is an orange bar in coalesced positions I + II + III which has the veins differentiated in black. Ventrally the dorsal pattern is reproduced but it is more pale and there is a yellow spot contained by the recurrent branch of the hindwing subcosta, a yellow forewing costal spot and a single row of paired intervenal white spots around the posterior margin of the hindwing. Females tend to be less heavily or richly marked than males but are similar in size, with a wingspan of approximately 72 mm.

In Central America the form *vialis* Stichel 1903:20 is known from southern Mexico to the borders of Colombia but south of Costa Rica it seems progressively replaced by *Heliconius edias vulgiformis*. Very few specimens that can clearly be assigned to *H. vibilius* are known from the central Colombian or Ecuadorian Andean valleys, from Venezuela or the Guianas, but from the Lower, Middle and Upper Amazon there is the stable form *vibilius* which is distinguishable from *vialis* only by the richer orange of the forewing bands, the more extensive orange over the forewing cubitus and by the vagueness of the posterior margin of the hindwing orange bar. In the upper tributaries of the Amazon the pattern becomes more richly orange and the distal forewing band is absent (*unifasciatus* Butler 1873:169).

In the valleys of the eastern Colombian, Ecuadorian and Peruvian Andes above 650 meters there is a high degree of variability but in general the orange markings are greatly extended so they may appear to form the ground color except in the position of hindwing bar III. Named forms included in this complex are *lampeto* Bates 1862:563, *fulginosus* Stichel 1903:12, *amoenus* Stichel 1903:13, *carbo* Stichel 1903:13, *apicalis* Röber 1927:402 and *acacates* Hewitson 1869b:22. An especially pale form from this area has been named *pallidus* Riffarth 1907:513. To the south in eastern and southern Brazil the distal band is retained though the color is still rich orange. Especially pale forms occur here too and have been named *pallens* Stitchel 1903:19.

The little known form *copiosus* Stichel 1906:57, which looks as if it should come from eastern Ecuador but carries the locality of British Guiana, is unlikely to be a series of labelling errors and may exemplify the extreme variability of this species, or it may be an interspecific hybrid between *H. vibilius* and *H. isabellae*. Only a female has been examined.

In the A.M.N.H. there is a single female specimen recorded from La Lechera, Rio Opon, north of Tunja, Boyaca, Colombia, which has typical *vibilius* morphology and ventral alary color pattern but which is dorsally similar to *H. lybius olympius*. There is a similar specimen in the B.M. from La Chima, which is in western Ecuador. Both localities have aberrent material in other species, so further specimens must be obtained before the distribution can be confirmed.

Specific Characters: The shape of the male genital valves (Text-fig. 33) together with the absence of androconia from all the forewing veins including 1A, and the extensive distribution of androconia over hindwing Rs (Text-fig. 76).

4. *Heliconius pavanus* Ménétriés 1857:116

Map 4: Text-figs. 33, 76, 148, 161

This species is known from a small number of specimens from eastern and southern Brazil. It is in appearance very like *H. vibilius vibilius*, with which it is partially sympatric, but it differs in that the hindwing has black intervenal spikes on both surfaces and the stems of hindwing veins M1 and M2 are retained and differentiated in black; the peripheral light spots on the hindwing are silver and in two sub-equally developed rows, the proximal of which are arranged in pairs so they look like blocks leaning against each other. The characters at the wingbase are as in *H. vibilius*. Females have the light markings a pale straw color whereas the males are

orange, but the sexes are approximately similar in size (wingspan 68-72 mm.)

Specific Characters: The signa of the female bursa copulatrix are reduced to short narrow bars with the deflection only just visible at the posterior extremity (Text-fig. 148), and the female foretarsi are similar to those of *H. alipherus* in that they lack a terminal spine (Text-fig. 15). The other characters including the shape of the male genital valves (Text-fig. 33) and androconia distribution are as in *H. vibilius* (Text-fig. 76).

5. *Heliconius lineatus* Salvin & Godman 1868:145

Map 4: Text-figs. 35, 77, 150

This species is very similar in appearance to *H. alipherus* but the dorsal and ventral ground colors are a richer orange and the dark markings are more extensive and more black. Ventrally there is a round yellow spot enclosed by the recurrent humeral branch of the subcosta and an elongate yellow spot in the angle between Sc + R1 and Rs. The forewing costal spot can barely be differentiated from the orange ground color. Females are larger (65-70 mm.) than the males (60-65 mm.), more pale and have the hindwing submarginal single row of white spots expressed weakly on the dorsal surface.

H. lineatus is confined to Central America where it is recorded from northern Panama to southern Mexico. The form *libitinus* Staudinger 1885-88:80 has not been seen.

Specific Characters: The restriction of androconia to hindwing veins Sc + R1 and to the proximal half of Rs (Text-fig. 77); the deflexed dorsal process of the ventral component of the male genital valves (Text-fig. 35) and the color-pattern.

6. *Heliconius eanes* Hewitson 1861:155

Map 4: Text-figs. 36, 77, 150, 161

All the known forms of this species seem sympatric and hence polychromatic but this can be attributed to lack of precision in the locality data, for they are all confined to the little-known eastern slopes of the Andes in Colombia, Ecuador, Peru and Bolivia. It is a small butterfly with a wingspan of about 64 mm.

H. eanes has an eastern interface with *H. tales* from which it can be immediately distinguished by the only single row of sub-marginal ventral hindwing spots, compared with the double row in *H. tales*. The cream forewing band is always compact and centered over the apex of the discal cell but it varies considerably in size by being composed of B alone, or A + B (Text-fig. 11). There is variable expression of a yellow and red costal spot, a hindwing costal streak which is yellow inside the humeral branch of the sub-costa and red beyond, and a group of red basal spots similar to those of *H. lybius lybius* but which are usually masked by ray (Text-fig. 119).

The known forms include *eanes* Hewitson 1861:155 which has a reduced forewing band distal to the discal cell (B), dennis (Turner & Crane, 1962) (Text-fig. 5) and full development of an *erato*-type ray (Text-fig. 6); *riffarthi* Stichel 1903:31 and *aides* Stichel 1903:30 without dorsal dennis or ray; *eanides* Stichel 1903:30 which is similar to *eanes* but with a larger band over the apex of the discal cell (A + B); *farragosus* Stichel 1903:30 with minimal dennis; *felderi* Stichel 1903:31 with a red forewing band and dennis but reduced ray; and *pluto* Stichel 1903: 32 with dorsally only a red band.

Data from museum specimens are vague but the most precise locality data are consistent with the situation that has been demonstrated in some sympatric dennis-rayed species like *H. erato* and *H. melpomene* (Emsley, 1964), in which the dennis and ray characters are typical of the lower altitudes and are lost at the higher levels in the river valleys. Though the museum data do not actively support the suggestion that the red banded forms are at the highest altitude, as in *H. erato* and *H. melpomene*, they do not preclude the possibility. It is interesting to note that the red-banded forms have the postero-dorsal process of the male valves more ventrally curved that the others. As in *H. tales*, the forewing band tends to become triangular in the Colombian Andes.

Specific Characters: The restriction of androconia to a barely perceptible line along Sc + R1 and the proximal half of Rs of the hindwing (Text-fig. 77), the male genital valves (Text-fig. 36) and the color-pattern.

7. *Heliconius isabellae* (Cramer 1781-82:117)

Map 5; Text-figs. 14, 37, 78, 150, 161

From the extreme south of the range of this species to the estuary of the Amazon river the form *dianasus* (Hübner 1806) has a small entire white or cream forewing band in position D (Text-fig. 11); a cream discal band in position A, broad orange lines over the cubitus and 1A, a variably developed cream hindwing bar in position II (Text-fig. 11) and an apically contiguous orange bar in position IV. The ground color is dark brown. The ventral pattern is similar but less intense and with a row of paired white dots in position V which are just visible dorsally and which are continued onto the tip

of the forewing. There is an orange forewing costal spot, and submarginal yellow hindwing costal streak and an occasional trace of a red basal spot in the angle between Sc + R1 and Rs.

Though connected to *dianasus* by intermediates, the characteristic form of the Guianas and the Amazon basin as far as the upper tributaries in the foothills of the Andes is *isabellae* (Cramer 1781-82: 117) which has both the discal and distal forewing bands broken into spots, the hindwing bar II is yellow or orange and the ground color remaining in position III is broken into spots. This form extends into the Magdalena and Cauca Valleys of northern Colombia, into western Colombia and marginally into western Ecuador.

At the extremities of the range in the eastern Andes, perhaps due to the relative isolation of the valley systems, above 650 meters there is considerable variation in the details of the color pattern but which in principle is due to an increase in the amount of orange. Named forms from these localities include *hippolinus* Butler 1873:169, *margaritiferus* Stichel 1903:5, *personatus* Stichel 1903:5, *brunneus* Stichel 1903:6, *dissolutus* Stichel 1903:6, *pellucidus* Srnka 1885:130, *olgae* Neustetter 1916:597 and *vegitissimus* Stichel 1903:8.

Around the spurs of the northern Andes there are detailed variations like *perimaculus* Boullet & Le Cerf 1910:25, *arquatus* Stichel 1903:9 and *spoiliatus* Stichel 1903:9 from the Cauca Valley and western Colombia; and *ecuadorensis* Strand 1912:181 from western Ecuador.

In Central America *H. isabellae* extends up as far as Mexico (*zorcaon* Reakirt 1866:243 and *adjustus* Stichel 1903:11) and almost certainly it is from this stock that Cuba and Puerto Rico have been colonized (*cleobaeus* Geyer 1832:7), as well as Hispaniola, where the light markings are all orange (*monochromus* Boullet & Le Cerf 1910:25). The island forms are usually smaller (60-72 mm.) than those from Central America (72-85 mm.) but similar to those from the South American mainland.

Specific Characters: The restriction of the androconia to hindwing veins Sc + R1 and Rs but with a spur along the Rs-M1 crossvein (Text-fig. 78); the very blunt and short upturned process of the dorsal component of the male genital valve (Text-fig. 37); and the color-pattern.

THE *LYBIUS* GROUP

Group features are the appreciably acute angle through which the slender signa is deflexed (Text-figs. 151-154); the lack of a hook on the ventral process of the male genital valves (Text-figs. 38, 39); the presence of androconia on the membrane in the vicinity of Sc + R1 and Rs. (Text-figs. 79, 80), and on forewing vein 1A; and the geniculate female abdominal processes (Text-fig. 169).

8. *Heliconius lybius* (Fabricius 1775:460)

Map 6; Text-figs. 38, 79, 119, 151, 152, 169

The dorsal color-pattern of this butterfly is basically similar to that of *H. alipherus*, but the dark markings are so much broader that the ground color appears to be the black rather than the orange. The forewing orange markings are restricted to a subterminal band, a very broad wedge-shaped arc over both branches of the cubitus and along the posterior border of the forewing. On the hindwing there is a large regular orange bar covering areas I-IV (Text-fig. 12) which is not invaded by spikes of peripheral brown as in *H. alipherus* and *H. lineatus*. The markings appear ventrally but, like the ground color, are very much paler. The females and males are approximately similar in size (65 mm.) but the color is less intense in the females.

The form *lybius* (Fabricius 1775:460) is widely distributed in the Guianas and Amazon basin. It is distinguished by a red forewing costal spot, a yellow hindwing costal streak and two or three red basal spots (Text-fig. 119). All the red spots are also expressed on the dorsal surface.

The apparent distributional continuity between *lybius* and *olympius* (Fabricius 1793: 166), which is known from northern and western Colombia, western Ecuador, northern Panama, Costa Rica and Nicaragua, is dependent upon very few specimens from the eastern Cordilleras. The form *olympius* is similar in pattern to *lybius* but lacks the red basal spots, has the forewing costal spot yellow and has the subapical forewing band pure white and more oval in shape. Some specimens of *olympius* from Central America, though typical in all other respects, have a small red spot on the dorsal surface of the location of the forewing costal spot in *lybius*.

The form *lybioides* Staudinger 1876:99 is similar to *olympius* but has the subapical forewing band a pale orange, and has a most interesting geographic distribution. Museum data labels give only Sevilla Island, Burica Island, Chiriqui, Veraguas, Bugaba, Lino and San Mateo, which with the exception of the slightly westward San Mateo are all on the southern slopes of the Chiriqui volcano or the nearby offshore islands. It has a distribution similar to that of *H. hewitsoni* and *H. pachinus*.

Specific Characters: The distribution of the androconia over the membrane as well as the veins in the region Sc + R1 and Rs, but with the androconia more heavily concentrated on the veins (Text-fig. 79); the shape of the male genital valves (Text-fig. 38) (the valves of the non-Amazonian *lybioides* and *olympius* have shorter dorsal processes than those of the Amazonian *lybius*); and the extremely acute angle through which the asymmetrical signa are curved (Text-figs. 151, 152).

9. *Heliconius tales* (Cramer 1775-1776:62 and 154)

Map 7; Text-figs. 10, 39, 80, 153, 154, 169

The most characteristic feature of this species is the double row of white spots in positions IV and V (Text-fig. 12) on the ventral surface of the hindwing. There is a yellow forewing costal spot and a hindwing costal streak which is proximally yellow and distally red. The macro-characters include dennis and the absence or variable development of a unique ray pattern which overlies the veins (Text-fig. 10); both characters may occur in combination with a spotted or compact cream forewing band.

In the Guianas and lower Amazon the characteristic forms are *surdus* Stichel 1903:27 with reduced ray and *tales* (Cramer 1775-78:62) with complete hindwing ray, both of which have dennis and the cream forewing bands broken into discrete spots. To the west of the lower Amazon the non-ray characters become less common and the forewing band becomes compacted so that near Teffé ray is almost always fully developed and the forewing band is more or less entire. Hence, the form *aquilifer* Stichel 1903:28, which has a partially coalesced forewing band without ray, is uncommon in this area whereas the rayed form *pythagoras* Kirby 1900:13 is more abundant. Westward from Teffé the forewing band is fully compact and always with ray and to the southwest the band lies beyond the discal cell *(calathus* Stichel 1909:178) whereas to the northwest in eastern Ecuador and Colombia it is centered over the apex of the discal cell *(heliconioides* C. & R. Felder 1861:102). As in the other yellow-banded dennis-rayed species the presence of ray and dennis breaks down in central Colombia and western Venezuela, and specimens with compact triangular forewing band and reduced ray are known from that region *(cognatus).*

In the northern Colombian forms like *crystalinus* Hall 1921:279 and *xenophanes* C. & R. Felder 1865:377 the ray is replaced by a solid proximal red area which appears to be composed of bars I-III (Text-fig. 12).

Some specimens of *H. tales* from Santarem have ray and dennis stone colored.

Specific Characters: The even distribution of the androconia over the veins and membrane on the Sc+R1 and Rs area of the hindwing (Text-fig. 80) and on vein IA of the forewing, the shape of the male genital valves (Text-fig. 39), and the shape of the signa (Text-figs. 153, 154).

Subgenus *Heliconius* Kluk 1802:82
Subgenotype: *H. charitonius*
(Linnaeus 1767:757)

Definition: *Heliconius* with a very short broad duct leading from the spermathecal diverticulum (Text-figs. 16, 17); five segmented tarsi on the female foreleg (Text-fig. 13); the presence of androconia on the membrane around the hindwing veins Sc + R1 and Rs as well as upon them (Text-figs. 30, 31); a 90 degree or less angle through which the symmetrical signa of the bursa copulatrix are curved (Text-figs. 26, 27); and finely pointed meso- and meta-pretarsal paronychia (Text-figs. 19-21).

THE *NATTERI* GROUP

Group features are the unique distribution of androconia over many hindwing veins without their encroachment onto the membrane (Text-fig. 81), the absence of signa (Text-fig. 28) and the almost straight female abdominal processes (Text-fig. 161).

10. *Heliconius natteri* C. & R. Felder 1865:375

Map 8; Text-figs. 45, 81, 120, 161

H. natteri is known only by a very few male specimens from Bahia in eastern Brazil. It is dark brown with a single oblique yellow forewing band distal to the discal cell, a broad yellow forewing line along the cubitus, and on the hindwing a dorsal and ventral yellow bar in positions II and III. There is a red costal forewing spot, a yellow hindwing costal streak, and a pair of red basal spots (Text-fig. 120).

H. fruhstorferi Riffarth 1899:406 is also known by very few specimens but which are all female and from either Esperito Santo or Pernambuco. The color pattern is similar to that of *natteri* except that the forewing line over the posterior margin of the forewing is orange, the yellow bar is restricted to position II of the hindwing and may be overprinted with orange, and there is an orange submarginal border to the hindwing in position IV. The minor characters are similar. The apparent allopatry of the sexes may not be a serious objection to their synonymic association for there are probably not more than

eight specimens of either sex known. The states of Bahia and Esperito Santo have a common boundary and the localities of *fruhstorferi* straddle that of *natteri*, so as acute sexual dichromatism is uncommon in *Heliconius* it is probable that they are dichromatic morphs not directly associated with sex, as is already known in *H. ethillus* and *H. isabellae*. Both sexes have a wingspan of about 80 mm.

Specific Characters: The group features serve also as specific characters together with the structure of the male genital valves (Text-fig. 45).

THE *HIERAX* GROUP

Group features are the androconia on the hindwing cubitus (Text-fig. 82), the short signa of the bursa copulatrix (Text-fig. 155), and the almost straight female abdominal processes (Text-fig. 161).

11. *Heliconius hierax* Hewitson 1869b:11

Map 2; Text-figs. 44, 82, 121, 155, 161

Heliconius hierax is known by a small number of uniform specimens from the valleys of the eastern Ecuadorian and Colombian Andes at altitudes between 1,000 and 1,300 meters. It is a medium-sized butterfly (wingspan 78 mm.) with yellow forewing bands in positions B and E, vague dennis posterior to the cubitus, and a red bar on the hindwing in coalesced positions I + II. The forewing bands are expressed ventrally together with a red forewing costal spot, but the hindwing has only a yellow costal streak, a red basal spot complex like Text-fig. 121 and paired intervenal white streaks emanating from submarginal white spots. The forms *semibrunneus* Niepet 1923:96 from Ecuador and *cinereofuscus* (Goeze 1779:122) from Surinam (!) have not been examined.

Specific Characters: The unique male genital valves (Text-fig. 44), together with the group characters.

THE *GODMANI* GROUP

Group features are the narrow arcuate signa (Text-fig. 156), the coarsely denticulate dorsal component of the male genital valves (Text-figs. 52, 53, 54), the extensive anterior area of the hindwing invested with androconia (Text-figs. 83, 84, 85) and the almost tubular spermatheca (Text-fig. 17). Each abdominal segment has a conspicuous yellow spot on the middle of each side. The female abdominal processes are strongly curved (Text-fig. 165).

12. *Heliconius godmani* Staudinger 1882:397

Map 8; Text-figs. 17, 52, 83, 156, 165

Heliconius godmani is one of the few species in the genus that has the alary color-pattern on both dorsal and ventral surfaces similar and equally well developed. The ground color is a matt dark brown with the forewing band composed of widely separate yellow spots, to which is added a submarginal single row of yellow fore and hindwing spots and an orange bar in hindwing positions II + III. There are no basal spots, only a vestige of a yellow forewing costal spot and a reduced hindwing yellow costal streak. *H. godmani* is known from very few museum specimens, all of which have been taken from near Rio San Juan in western Colombia. The sexes are alike and have a wingspan of about 80 mm.

Specific Characters: The isolated male genital valve (Text-fig. 52) is hard to distinguish from that of the other members of the group, but a valve of this type wedded to a *godmani* color-pattern is diagnostic as is the unique distribution of hindwing androconia (Text-fig. 83).

13. *Heliconius aoede* (Hübner 1816:12)

Map 9; Text-figs. 53, 85, 126, 156, 165

In the Guianas and along the lower tributaries of the Amazon the broken yellow forewing band combined with dennis may occur with an *erato*-type ray (Text- fig. 6) on the hindwing *(aoede)* or without one *(astydamius* Erichson 1848:595). As one travels westward towards Teffé, the frequency of the rayed individuals increases to 100% and the forewing band becomes compact and entire. The shape of the compact band may be short and broad *(bartletti* Druce 1876:219) or long and broad *(lucretius* Weymer 1890a:290) but both seem sympatric dichromatic forms occurring in the upper western tributaries of the Amazon up to about 800 meters. The more southern tributaries have the forewing band short and narrow *(cupidineus* Stichel 1906:31). The sexes are alike and have a wingspan of about 75 mm. All forms have a dark brown matt ground color, dennis, a reduced hindwing costal streak and pure white head markings. The forewing costal spot is masked by dennis so it is probably red and the basal spots are only faintly visible in non-rayed individuals (Text-fig. 126). Most specimens have more or less well developed paired intervenal white spots around the margin of the ventral surface of the hindwing. The rays are broader in the southwestern part of the range.

Specific Characters: The male genital valves are hard to distinguish from those of the

other members of the group (Text-fig. 53) but in combination with a dennis-ray color pattern they are diagnostic. The hindwing androconial distribution is also unique (Text-fig. 85).

14. *Heliconius metharme* (Erichson 1848:595)

Map 8; Text-figs. 54, 84, 156, 165

Heliconius metharme has a dark blue dorsal ground color with a barely perceptible iridescence and a pair of forewing bands in positions A (but not reaching the apex of the discal cell) and D. There is a very strong *erato*-type (Text-fig. 6) ray pattern on the ventral surface of the hindwing and a series of paired intervenal blue and white streaks on the dorsal surface, the distal extremities of which are expressed ventrally in white. The forewing costal spot and hindwing costal streak are both yellow and there is a forewing ventral yellow line posterior and parallel to the radius. The sexes are alike and have a wingspan of about 82 mm.

This species seems most common in the middle Amazonian region where it bears a strong resemblance to the sympatric *H. doris methariminae* but from which it may be distinguished by the more proximal position of the inner forewing band, the stronger ray pattern and the yellow forewing costal spot and hindwing costal streak.

Specific Characters: Though the genital valves are similar to those of the other species in the group, they are diagnostic in a dorsally blue butterfly (Text-fig. 54). The distribution of hindwing androconia is unique (Text-fig. 84).

THE *WALLACEI* GROUP

The group is characterized by the elongate shape of the denticulate dorsal process of the male genital valve (Text-figs. 40, 41, 42), the short posterior process of the signum and the rounded angle through which it is curved (Text-fig. 157), and the extensive distribution of androconia around Sc + R1 and Rs of the hindwing (Text-figs. 86, 87, 88). The ventral process of the meso and meta paronychia is about half as long as the dorsal process (Text-fig. 20), and the female abdominal processes are gently curved (Text-fig. 162).

15. *Heliconius wallacei* Reakirt 1866:242

Map 10; Text-figs. 20, 41, 86, 124, 157, 162

This is a large (82 mm. wingspan) dorsally iridescent blue butterfly with a discal and distal yellow forewing band in positions A and D, and a yellow line along the radius and cubitus veins. Ventrally there is a characteristic red basal spot complex (Text-fig. 124), a red costal spot on the forewing, a yellow and red hindwing costal spot enclosed by the recurrent branch of the humeral vein, a yellow line along the cubitus veins and a series of variably developed paired intervenal white streaks on the hindwing which emanate from marginal white spots.

Though of wide distribution in South America east of the Andes, there is geographic variation only in the shape of the forewing band A and in the prominence of the white streaks on the ventral surface of the hindwings. In the northern and northeastern parts of its range the forewing band is long narrow and rectangular *(wallacei)* (= *minulinus* Butler 1873:168); in Trinidad and the northeastern Guianas the band is basically similar to that of *wallacei* but is broader and more pointed at the posterior extremity (*kayei* Neustetter 1929:83), whereas in the southern Guianas, Lower Amazon and westwards to the slopes of the eastern Andes up to about 1,200 meters, though at this altitude the species is rare, the forewing band is broadly oval (*flavescens* Weymer 1890a:292). In the Guianas and Lower Amazon, forms in which the yellow of the forewing bands is replaced by white have been named *clytius* (Cramer 1775-76:103) and similar white-banded forms with the northern band shape are know as *elsus* Riffarth 1899: 407. From a number of localities in the Lower Amazon specimens are known in which the forewing band is variably reduced to two, three or four smaller rounded spots, named *colon* Weymer 1890a:291, *parvimaculatus* Riffarth 1900: 207, and *quadrimaculatus* Neustetter 1925:14, respectively. A specimen has been seen from British Guiana (B.M. Tring collection) in which the pair of forewing bands are enlarged and fused into a large rectangular cream band which occupies almost half the total area of the forewing. Another aberration is *halli* Kaye 1919:217 from Serpa which has a short narrow white discal band. Specimens have also been seen which lack the blue iridescence.

Specific Characters: Androconia on forewing veins M1, M2, M3, Cu1a, Cu1b and 1A, and on hindwing veins M1, M2, M3, Cu1a and Cu1b, and on Sc + R1 and Rs and on the membrane around them (Text-fig. 86); the shape of the male genital valves (Text-fig. 41); and the red basal spot complex (Text-fig. 124).

16. *Heliconius burneyi* (Hübner 1816:12)

Map 11; Text-figs. 42, 87, 125, 157, 162

Heliconius burneyi has a matt dark brown ground color with red dennis posterior to the subcosta, with or without hindwing ray and a variable yellow forewing band. The minor characters are a red forewing costal spot, a red and

yellow costal streak contained by the recurrent hindwing subcosta, a red basal spot complex as in Text-fig. 125, and paired white radiating streaks which emanate from white marginal spots on the ventral surface of the hindwing. The forewing costal spot and basal hindwing spots can be identified in individuals carrying dennis and ray by the magenta color of the red. The dorsal ground color lacks the iridescence of *H. wallacei* and the matt brown ventral ground color lacks the pearlyness of *H. egerius*. A further point of contrast with *H. egerius* is the less pointed but broader and more regular wing shape (Text-figs. 123, 125).

In the Guianas and Lower Amazon the forewing band is distinctly divided into a group of three yellow spots which may be combined with a very reduced ray pattern on the hindwing (*catherinae* Staudinger 1885:79) or with a fully developed *erato*-type ray *(burneyi)*, (see Text-fig. 6). Towards the western part of the range full development of ray becomes a constant feature and the forewing band becomes compact just proximal to the apex of the discal cell in position A (*huebneri* Staudinger 1896:312). In south-central Colombia, though the ray pattern is reduced almost completely, the forewing band is still compact (*lindigii* C. & R. Felder 1865: 377). There is variation in all localities in the density of expression of both dennis and ray on the ventral surface, but specimens from the extreme western situations have stronger rays and reduced forewing bands. The sexes are alike and have a wingspan of about 90 mm.

Specific Characters: The restriction of androconia to hindwing veins Sc + R1 and Rs and on the surrounding membrane in the pattern shown in Text-fig. 87, the shape of the male genital valves (Text-fig. 42), and the basal spot complex (Text-fig. 125) together with the presence of a red forewing costal spot.

17. *Heliconius egerius*
(Cramer 1775-76:54, 152)

Map 12; Text-figs. 40, 43, 88, 123, 157, 162

This species is very similar to *H. burneyi* in appearance but ventrally the wings are a pearly brown which is interrupted only by the forewing band, a yellow costal spot and hindwing costal streak, and faint basal spots in red (Text-fig. 123). In the Guianas and Lower Amazon the yellow forewing band is always broken up into separate spots over the positions A + B + C, but the hindwing may present a broad red dorsal bar which obscures or just does not obscure a reduced ray pattern *(egerius)*, or a fully developed *erato*-type ray which is usually without a bar (*hyas* Weymer 1884:26). A variety of *egerius* from French Guiana in which red markings are buff has been named *clearistus* (Oberthür 1923: 304). The status of *egerides* Staudinger 1896: 311 has not been ascertained. To the west of the range the forewing yellow band is rectangularly compact, almost entirely distal to the discal cell (positions B + C) and with a fully developed *erato*-type ray on the hindwing but without the basal bar (*astreus* Staudinger 1896:311).

Judging by museum specimens, *H. egerius* is not a common species and has been recorded only along the Amazon and its lower tributaries east of Sao Paulo de Olivenca and eastward into the Guianas. Though known from only a relatively small number of localities, it seems that broken band is characteristic of the Guianas and Lower Amazon and that full development of ray only rarely extends into this area where bar is common. The sexes are alike and have a wingspan of about 90 mm.

The form *astreus* is especially interesting for it has an additional dorsal process at the base of the male genital valve (Text-figs. 40, 43). Though such an intraspecific genital variation seems most uncommon in *Heliconius*, it is similar to that described in *Papilio dardanus* from west and east Africa (Turner, Clarke & Sheppard, 1961), and it does not seem a sufficient reason to erect a distinct species here. Unfortunately the number of specimens is small and the few specimens that are known from the likely intermediate localities have not been examined for this character.

Specific Characters: The male genital valves (Text-figs. 40, 43), the yellow forewing costal spot and the relatively extensive hindwing yellow costal streak, the wing shape (Text-fig. 123), the extensive distribution of androconia in the vicinity of Sc + R1 and Rs of the hindwing (Text-fig. 88), and the pearlyness of the ventral ground color.

THE *DORIS* GROUP

Group features are the relatively small curved signa of the bursa copulatrix (Text-fig. 27); the subequal paronychial processes (as Text-fig. 19); and the predominantly red hindwing costal streak (Text-fig. 122). The female processes are only gently curved (Text-fig. 163).

18. *Heliconius doris* (Linnaeus 1771:536)

Map 13; Text-figs. 7, 9, 27, 55, 89, 122, 163

The typical form of *doris* (= *caeruleatus* Stichel 1906:35) is a black butterfly with about an 86 mm. wingspan which has discal and distal yellow forewing bands in positions A and E, and with a more or less well developed hemistellate bright blue patch on the dorsal surface of the

hindwing (Text-fig. 9). Dorsally and ventrally the forewing has a yellow line along the cubitus and ventrally a red costal spot. The hindwing has a red, or red with minimal yellow, costal streak, a weakly developed *erato*-type red ray pattern which may obscure the red basal spots (Text-fig. 122), and variably developed paired intervenal ventral white streaks which emanate from paired white submarginal spots which are normally present on both wing surfaces. The hindwing also has paired marginal white fringing spots.

The typical blue form of *doris* extends commonly over the whole of tropical South America including the Amazon basin, the Guianas, Venezuela and the northeastern Andes. At the upper limits of the range in eastern Ecuador specimens are known in which the yellow of the forewing band is replaced by white (*gibbsi* Kaye 1919: 217), or is translucent (*tectus* Riffarth 1900: 207). The amount of blue is variable in all localities and the extreme of reduction in which the blue is barely perceptible has been named *metharminae* (Staudinger 1896:315) because of its similarity to *H. metharme* (No. 14).

North of western Venezuela into Central America, though the hindwing is still dorsally blue the discal yellow band is narrowed anteriorly over the apex of the discal cell and the ventral red rays are less strongly developed (*aristomache* Riffarth 1901:131). The reduction of the forewing bands may reach an extreme in which they are scarcely visible (*obscurus* Weymer 1890a:290), a condition which may also occur in the *doris* zone.

From Surinam to Nicaragua at variable but normally low frequency there are forms in which some of the blue scales of the hemistellate hindwing patch are replaced by green or yellow ones, though they are in other respects quite normal. Individuals may have the majority of the scales in this area yellow with the minority green (*viridis* Staudinger 1885-88:77), with the majority green and the minority yellow (*viridanus* Stichel 1906:35) or with the yellow, blue and green scales equally represented (*virescens* Riffarth). As judged by museum specimens, these green forms are most common in Panama and northern Colombia and experiments conducted in Trinidad (Sheppard 1963:148) have shown that the green form is truly polychromatic with both the blue and *erato*-rayed form (see *delilae* below), for at least two forms can be obtained from the same clutch of eggs. Also in Panama are specimens of *aristomache* in which there are some white scales mixed in with the hindwing blue (*luminosus* Riffarth 1901:132).

Throughout the Amazon and Orinoco basins there is a polychromatic character in which the blue of the *doris*-zone hindwing is overlayed by an *erato*-type (Text-fig. 6) red ray pattern, either completely (*delilae* (Hübner 1806-19)) or with the blue visible at the margins of the red rays (*amathusius* (Cramer 1777:124, 147)). Together with the *erato*-type ray there is a reddening of the dorsal surface of the forewing posterior to the radius as in "dennis" (Turner & Crane, 1962:144) (Text-fig. 5). North of northwestern Venezuela in the *aristomache*-zone there is also a red ray character, but in which the rays are comb-like (Text-fig. 7) and in which according to its development the underlying color may be completely obscured by the rays (*eratonius* Staudinger 1896:314, 317) or the blue or green may be marginally visible (*transiens* Staudinger 1896:314, 317). The presence of dennis in these rayed individuals decreases both in development and frequency as one proceeds north until in Nicaragua it is absent, hence the dennis associated with the northerly *eratonius*-type rays never reaches the intensity or extent of that associated with the southerly *delilae*-type rays.

Specific Characters: The shape of the male genital valves (Text-fig. 55); the unique blue or green ray pattern as in Text-fig. 9; and the predominently red hindwing costal streak (Text-fig. 122).

THE *HECUBUS* GROUP

Group features are the dense androconia along hindwing veins Sc + R1 and Rs and on the membrane around them (Text-figs. 90, 91); the shape of the male genital valves (Text-figs. 56, 57) and the almost straight female abdominal processes (Text-fig. 163).

19. *Heliconius hecubus* Hewitson 1857

Map 14; Text-figs. 56, 90, 99, 159, 163

This is a blackish-brown butterfly with a wingspan of about 85 mm. with only a trace of iridescence in the ground color. The forewing bands are narrow in positions C and E (Text-fig. 11) and show a strong tendency to break up into spots. There is also on the ventral surface of the forewing a pearly-yellow line just anterior to the cubitus and a brown costal spot. The hindwing has a broad yellow bar made up of coalesced radially elongate spots in position IV (Text-fig. 12), a submarginal border of paired intervenal white streaks and, ventrally only, a silver-yellow bar in position II which is separated from the yellow bar in position IV by russet brown in position III. There is also a pearly-yellow hindwing costal streak but no red basal spots.

Though the species seems confined to northern Colombia and the eastern slopes of the eastern cordilleras of Colombia and Ecuador, the

scanty locality data are difficult to interpret. It seems likely that the forms *hecubus, cassandrae* C. & R. Felder 1862:419, and *choarinus* Hewitson 1872:83 occur sympatrically in the lower Magdalena Valley and along the eastern Andes. At first sight they appear to differ markedly in the positions of the bars on the hindwing but the differences can be attributed directly to the variation in the length of the stems of the veins that bound the discal cell. In *hecubus* the discal cell is very small and hence exceptionally proximal in position, a trend that is present but to a lesser degree in *cassandrae* and *choarinus* so the elements of the hindwing pattern are more distal and less elongate. The form *choarinus* differs from *cassandrae* principally in that the brown between the yellow hindwing bars II and IV is continued round to position I anterior to the discal cell. The transitional stages can be seen in *intermedius* Riffarth 1907:509. The form *tolimus* Fassl 1912:55 is similar to *cassandrae* but the forewing bands are yellow and not white. Some specimens have a few yellow scales on the dorsal surface in the position of the forewing lines and hindwing bar II. These may be the heterozygotic expression of the characters discussed below.

From the Cauca, and perhaps from the Magdalena Valley too, there is a broken yellow banded form (*crispus* Staudinger 1885-88:76) which is like *choarinus* but the hindwing bar in position IV is reduced to a row of small spots and the yellow bar in position II is enlarged and expressed fully on the dorsal surface. The remaining light markings may be expressed in white (*crespinus* Krüger 1925:151), but either form may have the brown bar in position III extending into position I or not. The hindwing discal cell is normal in size.

Specific Characters: The male genital valves (Text-fig. 56) cannot be distinguished with certainty from those of *H. xanthocles* but the color pattern is diagnostic. The signa are broader, with up to eight rows of teeth, than any other species and are relatively larger (Text-fig. 159), and the forewing has androconia on many veins (Text-fig. 99).

20. *Heliconius xanthocles* Bates 1862:561

Map 14; Text-figs. 57, 91, 127, 158, 163

This species is one of the complex that has a yellow forewing band in combination with dennis with or without an *erato*-type ray (Text-fig. 6). It is essentially Amazonian though it extends into the Guianas where it is dichromatic in that *xanthocles* has a broken yellow band in position A–C, a distal band in position E (Text-fig. 11) and dennis but no ray, whereas the sympatric *valus* Staudinger 1885-88:78 is similar but with ray.

Towards the middle of the Amazonian region the forewing band becomes less broken (*paraplesius* Bates 1867:540) and always with ray, but in the upper Amazon, although ray is present, the yellow forewing band is unbroken, compact and without the outer yellow band (*melete* C. & R. Felder 1865:376).

H. x. xanthocles, valus and *paraplesius* are the only forms of any species in this complex which exhibit an outer yellow band with the exception of *H. melpomene* (?) *tumatumari* Kaye 1906:53 which may be the result of a wild cross between *H. melpomene* and *H. xanthocles*. The wingspan is about 72 mm.

Towards the extremities of the eastern upper tributaries but below 600 meters the forewing band becomes regular and either narrow (*melittus* Staudinger 1896:307), or broad (*melior* Staudinger 1896:307). The area of greatest variety is in south-central Colombia where dennis, ray and the compact forewing band facies disappear as in the other species in the complex.

In all *xanthocles* specimens there are intersegmental abdominal yellow annuli and outside the Guianas there is a small lateral yellow spot on each abdominal segment, but never as conspicuous as in *H. aoede* (No. 13). The light head markings are always all white. The forewing costal spot is masked by dennis so it is presumably red, the hindwing costal streak is red beyond the recurrent branch of the subcosta and yellow within, and the red basal spots can be seen only with difficulty in specimens carrying ray (Text-fig. 127).

Specific Characters: Though the male genital valves (Text-fig. 57) are similar to those of *hecubus*, there are no androconia on the forewing veins, and the signa are less gross (Text-fig. 158).

THE *NUMATUS* GROUP

Group features are signa with a well developed and sharply angled posterior limb (Text-fig. 26), androconia fairly evenly and heavily distributed over the hindwing veins Sc + R1 and Rs and the membrane around them (Text-figs. 92-97), male genital valves in which the dorsal processes lie clearly exterior to the lobose ventral processes (Text-figs. 46-51) and are only terminally denticulate. The hindwing costal streak is typically yellow and the forewing costal spot is red, the paronychial processes are subequal in length (Text-fig. 19) and the female abdominal processes are curved at their base (Text-fig. 164).

21. *Heliconius numatus*
(Cramer 1780-82:17, 251)

Map 15; Text-figs. 48, 92, 101, 164

This is one of the so-called "tiger" patterned species of *Heliconius* which are considered to mimic sympatric members of the distasteful groups Danainae and Ithominae. The pattern is composed of very variable areas of yellow or orange on a matt black ground color. The sexes differ only in that females are usually slightly more pale than males. The high degree of polychromatism together with most striking geographic differentiation makes the accurate description of the diversity of pattern and color excessively complicated. Here, only the more characteristic forms will be described, though the named varieties that belong to the species will be indicated together with their geographic distribution.

The gross range of *H. numatus* extends from southern Mexico to western Ecuador and on the eastern side of the Andes as far as southern Brazil. In southern Mexico, Guatemala, Honduras and Nicaragua the form *telchinius* Doubleday 1847:104 is monochromatic with a pair of yellow-spotted forewing bands in positions B and D (Text-fig. 11), and an orange base to the forewing posterior to the subcosta except for the black ground color over 1A and the proximal portion of the discal cell. On the hindwing there are orange bars in positions I + II and IV (Text-fig. 12). Ventrally the pattern is similar but with the addition of a series of paired intervenal white spots around the posterior margin of the hindwing and around the submargin of the forewing. There is also a variably developed single white spot posterior to the distal extremity of each of the hindwing veins Sc + R1 and Rs. There is a red forewing costal spot, a short hindwing yellow costal streak but no red basal spots. The wingspan is about 95 mm.

In a southerly direction through Costa Rica and Panama to northern Colombia, *telchinius* persists at a decreasing frequency in polychromatic complex which reaches monochromatic stability only in western Ecuador. There the form *metaphorus* Weymer 1884:24 is smaller (wingspan 85 mm.), lacks the discal yellow band (B) but has the distal half of the normally orange base to the forewing replaced by yellow (A), has reduced ground color markings on the forewing and has full development of bars I, II, III and IV on the hindwing.

The transitional forms from Central America and northern Colombia include *occidentalis* Neustetter 1928:258, *faunus* Staudinger 1885-88:74, *albofasciatus* Neustetter 1907:181, *hermanni* Riffarth 1899:407, *fasciatus* Salvin & Godman 1877:62, *defasciatus* Neustetter 1908: 264, *immoderatus* Stichel 1906:9, *clarescens* Butler 1875:223, *albucillus* Bates 1866:88, *ismenius* Latreille 1817:125 and *hoppi* Neustetter 1928:237.

Only very few specimens are known from Colombia east of the Andes and Venezuela but those that are known lead directly to the forms which are common in the Guianas and the Amazon estuary where there is considerable polychromatism in the expression of the discal forewing band and the hindwing bars. There are always three yellow distal spots which comprise the outer band D. These specimens rarely exceed a wingspan of 85 mm. The forms in the Guianese complex include *numatus, guiensis* Riffarth 1900:198, *melanopors* Joicey & Kaye 1916: 425, *melanops* Weymer 1893:304, *mavors* Weymer 1893:305, *bouletti* Neustetter 1928:239, *sylvaniformis* Joicey & Kaye 1917:89, and *diffusus* Butler 1873:168.

The last two forms named above are transitional towards *sylvanus* (Cramer 1781:143, 252) which occurs right across northern Brazil and leads to *braziliensis* Neustetter 1907:180, *hopfferi* Neustetter 1907:181 and *robigus* Weymer 1875:382 which extend around coastal Brazil to Santa Catharina. There is a dichromatic form of *robigus* in which the orange of hindwing bar I + II is yellow. This form *ethrus* (Hübner 1825:35) is analagous with *polychrous* in *H. ethillus.*

From the Amazon estuary the variation in a westerly direction is only moderate and such forms as *geminatus* Weymer 1893:299, *superioris* Butler 1875:224, *sincerus* Riffarth 1907: 501, *gordius* Weymer 1893:312, *zobrysi* Fruhstorfer 1910:194, *nubifer* Butler 1875:224, *mirificus* Stichel 1906:11, *prelautus* Stichel 1906: 10, *translatus* Joicey & Kaye 1917:91 and *talboti* Joicey & Kaye 1917:88 differ mainly in the proportions of orange to yellow on the forewings, the forms at the highest altitudes having the least yellow.

Specific Characters: The presence of androconia on forewing veins 1A, Cu1b, Cu1a, M3, M2, M1 and sometimes on R4 + 5 (Text-fig. 101), and on hindwing veins M1, M2, M3, Cu1a, Cu1b and the crossveins bounding the discal cell as well as over Sc + R1 and Rs and the membrane around them (Text-fig. 92). The male genital valves are similar to those of *H. ethillus* and *H. aristionus* but the ventral process is shorter and more rounded and the dorsal process is apically curved towards the midline (Text-fig. 48).

22. *Heliconius aristionus* Hewitson 1852

Map 16; Text-figs. 51, 93, 130, 164

This species is more restricted geographically than either of the other "tiger" patterned *Heliconius (H. numatus, H. ethillus).* In the eastern Andes and Upper Amazon it may reach a wingspan of 95 mm. but in the Middle and Lower Amazons it normally approximates to 85 mm.

Along the eastern slopes of the Andes from Bolivia to Colombia the forms occupying the highest altitudes, which in eastern Ecuador are 800 to 1,200 meters, are *aristionus,* the more red *splendidus* Weymer 1893:334, the more extensively orange *bicoloratus* Butler 1873:167 and the larger spotted *pratti* Joicey & Kaye 1917:90. All these forms are one shade of orange or red brown over the whole area covered by dennis and forewing bands A + B + C with a matt black ground color and have a red costal spot, a yellow and orange hindwing costal streak but no basal spots. The sexes are alike.

The data are vague on museum specimens but personal field experience suggests that the forms with the distal portion of the forewing band yellow are from slightly lower altitudes in Ecuador and Colombia (*messene* Felder 1862: 418) and are the transitional forms between the orange and black *aristionus* and the yellow, orange and black forms with barred hindwings that occur at the 600 meter level in Ecuador and at corresponding ecological levels to the north and south. These forms include *euphrasinus* Neustetter 1928:239, *lepidus* Riffarth 1907:503, *euphone* Felder 1862:418, *junctus* Neustetter 1925:11, *euphorbus* Stichel 1923: 261, *nephale* Seitz 1916:594, *gracilis* Riffarth 1907:504, *phalaris* Weymer 1893:334 and *euphrasius* Weymer 1890b:21, 116.

At 500 meters in eastern Ecuador the appearance is quite typical of all the Amazonian forms and though there is much variation in points of detail, the common features are a three spot distal yellow band on the forewing in position D and a yellow transverse band in position B (Text-fig. 11) which abutts against a more or less complete orange base to the forewing. The hindwing is almost completely orange with the ground color persisting only as a row of anteriorly truncate spots in position III and as a peripheral border. There are no white submarginal spots but some specimens have a single red basal spot (Text-fig. 130). Such Amazonian forms as these have been named *artemis* Riffarth 1907:502, *mirus* Weymer 1893:296, *sergestus* Weymer 1893:339, *peeblesi* Joicey & Talbot 1925:647, *nebulosus* Kaye 1916a:194, *aulicus* Weymer 1884:19, *tarapotensis* Riffarth 1901:59, *timaeus* Weymer 1893:331, *lenaeus* Weymer 1890:284, *idalion* Weymer 1893:337, *confluens* Neustetter 1912:55, *obscurior* Stichel 1906:15, *subnubilis* Stichel 1906:14, *ignotus* Joicey & Kaye 1917:89, *humbolti* Neustetter 1928:442, *alexander* Neustetter 1928:442. Some specimens from this region have the dark markings excessively large, the normally yellow markings almost completely orange and the orange pattern a red-brown. Examples of these are *pardalinus* Bates 1862:555, *lucescens* Weymer 1893:321, *aurorus* Bates 1862:555, *leopardus* Weymer 1893:319, *hippolus* Hewitson 1867a, *lyrcaeus* Weymer 1890a:286, *elegans* Weymer 1893:326, *arcuellus* Druce 1874:156, *seraphion* Weymer 1893:330, *radiosus* Butler 1873:166, *coloratus* Stichel 1919a:119, *dilatus* Weymer 1893:323, *maeon* Weymer 1890a:287, *tithoreides* Staudinger 1900:404, *garleppi* Neustetter 1928:239 and possibly *pretiosus* Weymer 1893:325 and *staudingeri* Weymer 1893:324.

Though occurring at low frequency in the Upper Amazon, the forms *isabellinus* Bates 1862: 554, *floridus* Weymer 1893:329 and *gradatus* Weymer 1893:353 are more common at the lower levels, where they form a link with the Lower Amazonian and marginally Guianan forms *paraensis* Riffarth 1900:197, *latus* Riffarth 1900:197, *thielei* Riffarth 1900:195, *xinguensis* Neustetter 1925:11, *schulzi* Riffarth 1899:405 and *novatus* Bates 1867:539.

Specific Characters: The presence of androconia on hindwing veins M1, M2, M3, Cu1a and Cu1b but not on the veins bounding the discal cell, and on Sc + R1 and Rs and on the membrane around them (Text-fig. 93); there are forewing androconia only on vein 1A. The male genital valves (Text-fig. 51) are barely distinguishable from some of the other members of the group. Females are almost impossible to assign to species unless with a characteristic form of wing pattern.

23. *Heliconius atthis* Doubleday 1847:102

Map 16; Text-figs. 50, 95, 129, 160

This butterfly has a matt black ground color with a yellow band near the middle of the discal cell of the forewing (proximal to position A, Text-fig. 11), a dorsal and ventral forewing yellow line over the cubitus, a white fleck between the origins of R1 and R2 (position B) and on the hindwing a yellow bar in position II and a row of yellow and white spots in position IV which are continued onto the forewing. Ventrally only there is a row of russet spots in position V which also run onto the forewing, and a series of paired intervenal marginal white spots. There is a red forewing costal spot, a yellow hindwing costal streak and a single red basal spot (Text-fig. 129).

The species is geographically restricted to western Ecuador below 500 meters where it is common and occurs with the similar patterned *H. charitonius peruvianus* (No. 38). The sexes are alike, very stable and have a wingspan of about 76 mm.

Specific Characters: Within the group the color pattern is the only diagnostic feature for the male genital valves (Text-fig. 50) are similar to those of some of the other members as is the distribution of hindwing androconia (Text-fig. 95). The larger radius of curvature of the signa (Text-fig. 160) is barely detectable.

24. *Heliconius ethillus* Godart 1819:219

Map 17; Text-figs. 49, 94, 100, 130, 164

This is a "tiger" patterned *Heliconius* which, like *H. numatus,* ranges from southern Mexico, where it has a wingspan of about 95 mm., to western Ecuador and southern Brazil where it is about 10 mm. smaller. The geographic variation is considerable and, together with the widespread polychromatism, makes the description and identification of named forms very complex. The sexes are similar but females tend to be larger and more lightly marked than males. The minor characters are relatively constant and include a red forewing costal spot, a yellow hindwing costal streak and a single red basal spot (Text-fig. 130), and paired intervenal marginal white spots around the posterior border of the hindwing.

In southern Mexico, Guatemala, western Honduras and Salvador the form *fornarinus* Hewitson 1854 is monomorphic and dorsally black with a broken yellow forewing band in positions D + E and a more or less complete yellow band in position A + B. Ventrally the forewing pattern is expressed together with a pair of russet bars on the hindwing in positions I + II and IV, and a single white submarginal spot posterior to the extremities of each of the veins Sc + R1 and Rs. The form *styx* Niepelt 1921:19 has the forewing markings transluscent.

From Honduras there is a substantial change in the appearance for *fornarinus* becomes an uncommon element in a polychromatic population which, through intermediates like *discomaculatus* Weymer 1890a:289 and *chrysantis* Godman & Salvin 1881:146, merges into *zuleikus* Hewitson 1854 which is the characteristic form of Costa Rica and Panama. Typically *zuleikus* has completely spotted forewing bands, an orange base to the forewing posterior to the cubitus, and hindwing bars I + II + III + IV, but it occurs with other forms which have the forewing bands white and with varying stages of reduction of the orange bar III *(albipunctatus* Riffarth 1900:199, *xanthicus* Bates 1864:57, *jucundus* Bates 1864:56 and *dentatus* Neustetter 1907:183).

At low frequency in Panama, but more commonly in northern Colombia, the discal yellow forewing band becomes more compact like the Guatemalan *fornarinus,* and the distal yellow band is reduced to a single row of three spots. These forms vary considerably in detail, particularly in the development of the hindwing bars, and include *claudiae* Godman & Salvin 1881: 145, *melicertus* Bates 1866:87, *zygius* Riffarth 1907:504, *muzoensis* Neustetter 1908:226, *semiphorus* Staudinger 1896:284, *holcophorus* Staudinger 1896:285, *eucherius* Weymer 1906:70, *rebeli* Neustetter 1907:182, *semiflavidus* Weymer 1893:302, *depunctus* Boullet & LeCerf 1909:461, *orchamus* Weymer 1912:73 and *juntanus* Riffarth 1900:196.

On the eastern slopes of the Colombian Andes and extending around the Guianian Highlands to the Guianas and the Amazon estuary, the forms recognized in northern Colombia become modified to forms like *estebanus* Kaye 1913: 132, *anderidus* Hewitson 1852, *metalilis* Butler 1873:167 and *mentor* Weymer 1884:22, which differ in that there is a row of ground color spots in hindwing position III, the forewing band is more convex distally and the interface between the yellow and the orange is more diffuse.

In eastern Venezuela, Trinidad and the Guianas there are dichromatic forms in which the orange of the forewing is partially replaced by yellow and the hindwing bar II is more or less all yellow. Forms with excess yellow are *ethillus* Godart 1819:219 and *flavofasciatus* Weymer 1893:303. In Trinidad the specimens previously referred to as *"numata"* should more correctly be designated *H. ethillus ethillus* for the yellow form and *H. ethillus metalilis* for the brown form. The genetics of this dichromatism has been studied by Sheppard (1963) and Turner (unpublished).

In the Guianas and Lower Amazon there are a series of forms which differ principally in the nature of the interface between the yellow and the orange of the forewing bands and in the variety of expression of the hindwing bars. These forms include *eucomus* Hübner 1816:11, *sulphureus* Weymer 1893:311, *hyalinus* Neustetter 1928:238, *cephallenius* Felder 1865:373, *numismaticus* Weymer 1893:303, *vetustus* Butler 1873:165, *metellus* Weymer 1893:290 *boyi* Röber 1923:57. These forms have become more stabilized in the Middle Amazon in *spurius* Weymer 1893:309, *fortunatus* Weymer 1884: 21, *ennius* Weymer 1890a:283, *nigrofasciatus* Weymer 1893:307 and *aerotome* Felder 1862:

79, but in the upper tributaries they become more discretely differentiated into *tyndarus* Weymer 1896:317, *versicolor* Weymer 1893: 317, *concors* Weymer 1893:317, *jonas* Weymer 1893:308, *sisyphus* Salvin 1871:413, *clarus* Michael 1926:191 and *felix* Weymer 1893:315 from the Bolivian and Peruvian Andes; *quitalenus* Hewitson 1852 from eastern Ecuador; and *ithacus* Felder 1862:418, *hero* Weymer 1912: 75, *cajetani* Neustetter 1908:265, *vittatus* Butler 1873:166, *sulphureofasciatus* Neustetter 1925: 11, *nigroapicalis* Neustetter 1925:12, *indecisus* Joicey & Kaye 1917:91 and *marius* Weymer 1890b:116 from the eastern valleys of central Colombia. These last-named forms merge into those already mentioned from northern Colombia and Venezuela. None of these forms reach the altitudes attained by *H. aristionus*.

From the Amazon estuary there is a cline in a southeasterly direction leading around the coast of Brazil as far as Santa Catharina. The characteristic form is *narceus* Godart 1819:217 which is distinguished by the distal forewing band being entire and white and the hindwing bars I + II and IV being fully represented. There are transitional forms like *brunnescens* Neustetter 1907:180 and *flavomaculatus* Weymer 1893: 340 in which the entire distal band is yellow. The dichromatism noted in Trinidad occurs in Brazil too, the forms *polychrous* Felder 1865: 375 and *physcous* Seitz 1913:378 having excess yellow on the forewing and the hindwing bar II fully yellow. There is excess of orange in *satis* Weymer 1875:380.

Specific Characters: The presence of androconia in males only on the forewing vein 1A and the posterior margin (Text-fig. 100) and only on hindwing veins Sc + R1 and Rs and on the membrane around them. (Text-fig. 94). The male genital valves are a poor character for in the Amazonian and Brazilian populations the dorsal process is not so elongate as in the Central American forms (Text-fig. 49) and there is likely to be confusion with those of the other species in the group. Females are difficult to assign with certainty in the Amazonian and Guianian regions.

25. *Heliconius hecale* (Fabricius 1775a:254)

Map 21

This is a most easily recognizable species as it carries on its black ground color only a white forewing band in position A + B and a trio of white spots in position D. A pair of specimens from El Chorr, Venezuela, have the proximal band in position B + C. Ventrally there is in addition a russet forewing costal spot and line along the radius, and on the hindwing a yellow costal streak and a row of paired intervenal white spots around the posterior border. Some specimens show a faint ventral russet bar in positions I + II and IV as in *H. ethillus fornarinus* and *H. cydno*. The form *clearei* Hall 1930: 278 differs only in the details of the forewing band but *fulvescens* Lathy 1906:452 has a red-brown base to the forewing and a red dorsal bar in position I.

It is a large butterfly with a wingspan of 90 mm. which is known only from a few localities in British Guiana, southeastern Venezuela, and possibly Surinam and French Guiana. There is a unique specimen in the collection of Barcant (see page 192) which was authentically taken near Rio Claro in Trinidad, but it is assumed to have been an accidental introduction.

It is not known to what degree if any *H. hecale* is geographically or ecologically isolated from ostensibly sympatric forms of *H. ethillus*, to which it is undoubtedly very closely related.

Specific Characters: It is morphologically indistinguishable from *H. ethillus*, so the alary color pattern is the only character known to be of value.

26. *Heliconius elevatus* Nöldner 1901:5

Map 19; Text-figs. 49, 93, 130, 160

This species is easily confused with *H. melpomene*, as all the major components of the alary color pattern are similar, even including the association of hindwing bar I with forewing dennis and the hindwing ray pattern (Text-fig. 8). In a previous paper (Emsley, 1964), *H. elevatus elevatus* and *H. e. perchlorous* were included in *H. melpomene* in error.

H. elevatus seems restricted to the Upper Amazon and the Andean valleys of Ecuador, Peru and Bolivia. As is consistent with the other dennis-rayed species that inhabit these areas, the yellow forewing band is more or less compact and centered over the apex of the discal cell at the lower altitudes and distal to it at the higher ones. All the known specimens have dennis and ray expressed or both wing surfaces and ventrally the forewing costal spot is obscured by dennis, so it is presumably red; the hindwing costal streak is totally red, there is an arcuate yellow line just posterior to the proximal half of Sc + R1, the red bar I is expressed narrowly and there are paired white submarginal spots around the posterior border of the hindwing. The light head markings are all white. There is one basal spot as Text-fig. 130.

There is a long series of specimens in the A.M.N.H. collection from Mt. Roraima, which is near the Brazilian and British Guianese border, which have all the morphological and

alary features of *H. elevatus* except that ray is only expressed by a row of small spots which represent the bases of the rays. The forewing band is slightly more disperse. Temporarily these forms are allocated to *H. elevatus*. The forms *perchlorus, schmassmani* and *aquilinus* have not been re-examined but probably belong to *H. elevatus*.

Specific Characters: The presence of androconia on hindwing veins M1, M2, and M3 as well as on Sc + R1 and Rs (as Text-fig. 93); the shape of the genital valves which are indistinguishable from those of *H. ethillus* (Text-fig. 49); the unusually large radius of curvature of the signa (as Text-fig. 160); the red hindwing costal streak; and the yellow line posterior to the proximal ventral margin of Sc + R1 on the hindwing.

27. *Heliconius melpomene* (Linnaeus 1758:467)
Map 18; Text-figs. 8, 19, 26, 46, 96, 131, 164

This species, together with *H. erato,* is exceptionally strongly differentiated into geographic races which in the areas between contrasting zones are highly polychromatic (Emsley, 1964).

In western Ecuador, Colombia, Central America, Venezuela, Trinidad, southern Brazil, southeastern Bolivia and in the deeper valleys of the eastern Andes the forewing band is always red, but in the Amazon basin it is usually yellow as is the forewing band of all the other species of *Heliconius* in that region, with the exception of *H. hermathenae*.

In western Ecuador and western Colombia there is a yellow bar on the ventral surface of the hindwing in position II (Text-fig. 12) to which is added a similarly located dorsal bar in northern Colombia, Central America, southern Brazil, eastern Bolivia and the valley of the Huallaga River in eastern Peru. There is a decreasing cline in the intensity of the blue iridescence from western Ecuador through northern Colombia into Panama and Venezuela.

In the Guianas there is a polychromatic population exhibiting the red forewing band, which is typical of the northern races, in a large variety of combinations with the broken yellow band which is the characteristic feature of the populations of the Lower Amazon. All these combinations may occur with or without dennis, which in *H. melpomene* has associated with it a red hindwing bar in position I. Those with dennis may or may not have radiating red rays on the hindwing (Text-fig. 8). As one proceeds westwards the combination of dennis and ray becomes more frequent until at Obidos and beyond all specimens carry both. Simultaneously the distinct group of forewing yellow band spots begin to become coalesced, so by Teffé it is a compact yellow rectangle almost completely distal to the discal cell.

In the valleys of the eastern Andes at about 650 meters the yellow forewing band becomes discretely double and at about 850 meters the color changes to red and white and dennis and ray are lost. The altitudes quoted are based on personal observation in the Pastaza valley in eastern Ecuador and may differ from those of other valley systems. At about the 1,300 meter level in the Pastaza valley the *timaretus* Hewitson 1867:563 complex is exceptional, for the members of it have a yellow forewing band and either dennis and ray or ray alone (Text-fig. 8). There are no other races known in which ray occurs in the absence of dennis.

Each of the major valley systems of the eastern Andes has a characteristic forewing band shape. The broad bicolored red and yellow band of *heurippus* Hewitson 1854 is from the Guatiquia River in eastern central Colombia; the double yellow band is from the Pastaza River in eastern Ecuador between 650 and 850 meters, and above this altitude it becomes red and white or all red (*plesseni* Riffarth 1907:333); the Morone River in southeastern Ecuador is characterized by a single distal oval yellow forewing band (*ecuadorensis* Neustetter 1908:267); the Huallaga River forms have a large single red band (*amarylis* C. & R. Felder 1862:80) as do those of the Upper Madre de Dios River (*euryades* Riffarth 1900:205), wheras those from the Perene River (*xenocleus* Hewitson 1852) have large double all-red forewing bands. The details of these races have been presented in Emsley, 1964.

So, in addition to the Guianas, it is in east-central Colombia, the eastern Andes and in central Bolivia that polychromatism is known, that is, where the apparently stable Amazonian forms meet the contrasting and stable peripheral populations. In almost all forms the minor characters are relatively constant, for there is always a red forewing costal spot and yellow hindwing costal streak and the only exceptions to the basal spot complex (Text-fig. 131) are some of the forms isolated in the Huallaga and other Peruvian river valleys. In these cases specimens from the highest altitudes lack the spots, which are a variable feature in those from intermediate levels.

The forms *rubellius* Grose Smith & Kirby 1892, *wernickei* Weymer 1906:8 and *emilius* Weymer 1912:73 are held to interspecific hybrids between *H. melpomene heurippus* and *H. cydno,* whereas *seitzi* Neustetter 1916:594 is a

rare intraspecific hybrid between *H. melpomene heurippus* and *H. melpomene rosinus*. The characters of these forms are all either intermediate between or combinations of those possesssed by the suggested parental stock.

The Guianian forms *tumatumari* Kaye 1906: 53 (without ray) and *bari* Oberthür 1902:23 (with ray) both possess a distal forewing yellow band in addition to the broken yellow discal band and are held to be interspecific hybrids between *H. melpomene* and *H. xanthocles*. The breeding capacity of these postulated wild hybrids is unknown.

In a recent communication, Dr. K. S. Brown[8] has suggested that, contrary to the view expressed in Emsley (1964), *besckei* may be specifically distinct from *H. melpomene nannus*. Both species appear to fly together near Brasilia and on the east coast of Brazil, without the presence of specimens carrying intermediate or recombined characters.

Specific Characters: In respect of the group characters like the signa (Text-fig. 26), female abdominal processes (Text-fig. 164) and hindwing androconia (Text-fig. 96), *H. melpomene* is quite typical and the only specifically useful features are the male genital valves (Text-fig. 46), the basal spots (Text-fig. 131) and the color pattern.

28. *Heliconius cydno* Doubleday 1847:103
Map 19; Text-figs. 26, 47, 97, 164

Over its whole range the color pattern of this species is subject to considerable geographic and polychromatic variation, most of which seems correlated with that of *H. sapho* (No. 45). The wing span of *H. cydno* approximates to 85 mm., but some of the valley forms may reach 95 mm.

The most northern form (*galanthus* Bates 1864:58) extends from British Honduras through Guatemala, Honduras, Nicaragua and Costa Rica. It has a bright blue iridescent dorsal ground color with a single broad white distally convex forewing band which is slightly incised at the antero-dorsal angle of the discal cell. The hindwing has a weak white border of rectangular submarginal spots in position IV (Text-fig. 12) which merge into a more strongly developed apical row in position V. Ventrally the dorsal pattern is expressed together with a yellow hindwing costal streak and a pair of russet bars in positions I and III which form a nearly closed U-shape. There is no forewing costal spot and no trace of hindwing red basal spots.

At low frequency in Nicaragua and Guatemala the forewing band may be apically truncate and yellow (*diotrephes* Hewitson 1869a:33) but with typical *galanthus* hindwing spots. From Costa Rica to northern Colombia the hindwing spots become more strongly developed by the addition of a second row in position V which are more pronounced posteriorly. These are associated either with a yellow apically truncate forewing band or with a white distally convex band which may be large (*chioneus* Bates 1864: 58) or small (*exornatus* Riffarth 1907:505).

The variation in forewing band and hindwing border is carried into northern Colombia where at the entrance to the Cauca and Magdalena Valleys the characteristic type has a broad truncate yellow band with a very strong hindwing border consisting of large white submarginal rectangular spots (*cydno*). This form extends down the valleys and over the western and eastern cordilleras but its identity becomes lost in combinations with other forms. On the western side of the western cordilleras in Colombia the dominent form is *zelinde* Butler 1869:17 which has an apically truncate yellow band and very weak white spots which are posteroventrally confluent with fringing white scales as in *galanthus*. Further south the hindwing border becomes much more strongly expressed and in western Ecuador it is a broad complete border formed by coalesced bands III + IV + V. Forms with this hindwing border are *alitheae* Hewitson 1869b:10 which has a single yellow forewing band emarginated in the discal cell, *neustetteri* Riffarth 1908:114 which has the band partially divided into three components, *egregius* Riffarth 1907:505 in which the three spots are separate, and *haenschi* Riffarth 1900:200. The form *aventinus* Oberthür 1925:82 has the forewing bands completely double and white but retains a hindwing border like *alitheae*.

In western Colombia there are a large number of forms recorded which have various combinations of forewing band and hindwing border, for example, large yellow band with reduced white border (*bronchus* Stichel 1906:21), fully confluent double yellow bands and hindwing spots barely visible (*flavidior* Neustetter 1928:258), double yellow bands with hindwing spots which are small (*subcydnides* Staudinger 1896:289), medium (*cydnides* Staudinger 1885-88:77) or large (*epicydnides* Staudinger 1896:289), double white bands only (*albidior* Neustetter 1928: 259), double white forewing bands and medium width border (*aztekus* Neustetter 1928:259),

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and posteriorly confluent double white forewing bands and medium width hindwing border (*confluens* Neustetter 1928:259).

In the terminal reaches of the Cauca Valley there is a form with a virtually bandless forewing and on the hindwing only a yellow bar in position II (*gustavi* Staudinger 1896:287). This occurs together with forms in which the forewing band shows characters which are intermediate between either total absence and a divided white band (*weymeri* Staudinger 1896: 287), or absence and a spotted white band (*submarginatus* Fassl 1912:56). All these forms show only a suspicion of the ventral russet U-shape bars and the ventral costal streak.

In the Magdalena Valley there is a series of forms in which the forewing band is broken up into small spots with an additional submarginal row of dots around the forewing margin. The hindwing border in position IV is yellow. The forewing band may be white or yellow and white (*hermogenes* Hewitson 1857), or yellow (*lutescens* Kaye 1916a:194). Specimens exist in this locality (*temerindus* Hewitson 1873) in which the white forewing band is intermediate between the broken band of *hermogenes* and the broad single band of *chioneus*.

If locality labels are to be trusted, some of the characters which are typical of the Cauca and Magdalena Valleys have spread slightly over the cordilleras, which one would normally expect to limit them. This is supported by forms like *submarginatus* which combine weak expression of the *hermogenes*-type Magdalenan forewing band with the Caucan hindwing bar II. *H. cydno* may then be capable of existing at higher altitudes than *H. melpomene* and *H. erato*, both of which seem to find the Colombian cordilleras insurmountable barriers. This would suggest that the interspecific hybrids postulated when discussing *H. melpomene* have been made possible by invasions of *H. cydno* into the Guataquia Valley, where *heurippus* is found, rather than the other way around.

It seems from the foregoing that none of the named forms are monochromatically typical of any one locality. In each area the species is at least dichromatic with respect to either forewing band, or hindwing border or both. Genotypic recombinations may give rise to either recognizably intermediate characters or discrete phenotypic recombinations, hence the large number of named forms. The forms *cydnides, epicydnides* and *subcydnides* have a wide distribution in Colombia, as they are the double yellow band character combined with a series of expressions of hindwing border. The most characteristic forms seem to be *galanthus* from Central America, *chioneus* and *cydno* from northern Colombia outside the upper reaches of the river valleys, *hermogenes* in the Magdalena Valley, *gustavi* in the Cauca Valley, *zelinde* in western Colombia and *alitheae* in western Ecuador.

Specific Characters: As in *H. melpomene*, the group features provide little of specific value (Text-fig. 97) and the male genital valve (Text-fig. 47) cannot be distinguished from that of *H. pachinus*. The ventral hindwing russet U-shape bars are useful but occur also in *H. ethillus fornarinus* and very faintly in *H. hecale*.

29. *Heliconius pachinus* Salvin 1871:414

Map 16; Text-fig. 26, 31, 128, 164

This species shares its very restricted geographic distribution with the similarly colored *H. hewitsoni*. Data labels examined have revealed Chiriqui Volcano as the most common locality, together with the off-shore islands of Brava, Sevilla, Parida and Taboga. Other localities include Veraguas and Lion Hill in Panama, and San Mateo, Pozoazul and Corillo in Costa Rica.

The species differs from the sympatric *H. hewitsoni* principally in the smaller size of the red basal spot in the angle between Sc + R1 and Rs (Text-fig. 128), the lack of a yellow line along the ventral surface of the forewing radius, and the more distal positions of both the outer (E) and inner (B) forewing bands. Both species have a red costal spot and a yellow bar on the hindwing in position III. There is a red hindwing costal streak. The wingspan approximates to 85 mm.

Specific Characters: The group features are expressed quite typically, and morphologically *H. pachinus* differs from *H. cydno* only in that the androconia on the hindwing from a hooked pattern distally (Text-fig. 31), but this pattern also occurs in *H. cydno weymeri* so the only characters of real value are the color pattern and the unique red basal spot complex (Text-fig. 128).

THE *HECALASIUS* GROUP

Group features are the lack of signa on the bursa copulatrix (Text-fig. 28); the poor development of the dorsal process of the male genital valves (Text-figs. 58-63, 65-66); the 2:1 proportions of the lengths of the paronychial processes (Text-fig. 20); the lack of androconia on the forewing veins and their presence on hindwing veins Sc + R1 and Rs, on the membrane around them and usually on some other hindwing veins (Text-figs. 102-108, 110); and the curved female abdominal processes (Text-figs. 165-168) with the exception of *H. telesiphe* (Text-fig. 171).

30. *Heliconius hecalasius* Hewitson 1853
Map 20; Text-figs. 58, 103, 166

This species extends from the Magdalena Valley in northern Colombia, where it occurs with the rather similar *H. cydno hermogenes*, through Central America as far as Mexico, where sexual dichromatism is much more pronounced than in the south. Females are more pale than males and have a more yellow antenna.

In the Magdalena Valley *hecalasius* has a non-iridescent black ground color with scattered yellow band spots and a peripheral row of submarginal yellow spots on the forewing, and on the hindwing a row of yellow spots in position IV which enclose a russet patch which is most intense at the anal angle. There is a yellow and brown forewing costal spot and hindwing costal streak but no basal spots. The only known locality datum for *gynaesius* is Colombia, which if accurate is most likely from the Cauca Valley. The type has not been seen, nor any other specimen.

To the north in Panama, Costa Rica and Nicaragua *formosus* Bates 1863:247 has a greatly increased amount of orange on the hindwing with consequent reduction in the size of the bar IV yellow spots, and there is a trace of orange at the base of the forewing posterior to the cubitus.

In Guatemala, Honduras and southern Mexico this trend is continued in *octavius* Bates 1866:86 which has even more orange and smaller spots on the hindwing, more discrete oblique forewing bands and more extensive orange at the base. It is a pattern that is not greatly dissimilar from that of the sympatric *H. lineatus*.

Specific Characters: The male genital valves (Text-fig. 58) are hard to distinguish from those of *H. longarenus* (Text-fig. 59) but only *H. hecalasius* has androconia on M1 and M2 of the hindwing (Text-fig. 103) which are most prominent on northern specimens; the female processes are strongly curved (Text-fig. 166).

31. *Heliconius longarenus* Hewitson 1875:182
Map 20; Text-figs. 59, 104, 166

This species is known only by a few specimens from western Ecuador and western Colombia. The rather elongate forewings have a span of about 90 mm. and the black non-iridescent ground color carries a broad orange line over the cubitus and a pair of oblique yellow bands in positions B and D (Text-fig. 11), the distal of which is continuous with a row of submarginal yellow spots around the border of the wing. On the hindwing there is an orange bar in position II (Text-fig. 12) and a row of yellow spots in position IV. The forewing costal spot and hindwing costal streak are yellow and brown and there is a white spot over the origin of the cubitus and Rs. The appearance is generally similar to that of *H. hecalasius octavius* or *gynaesius*.

Specific Characters: The male genital valves (Text-fig. 59) are useful when combined with the absence of androconia from hindwing veins other than Sc + R1 and Rs (Text-fig. 104). The female processes are strongly curved (Text-fig. 166).

32. *Heliconius hermathenae* Hewitson 1853
Map 21; Text-figs. 61, 108, 136, 168

This red-banded species is particularly interesting for its limited distribution along the lower-middle Amazon where its sympatric species of *Heliconius* are all of much wider range and few of which exhibit a red forewing band. In appearance *H. hermathenae* is very similar to *H. charitonius* in that it has a broad yellow forewing line over the cubitus, a red forewing costal spot, a yellow hindwing costal streak, a group of basal spots, some of which are expressed dorsally, a yellow hindwing bar in position II and rows of yellow dots in positions IV and V. But it differs markedly by the replacement of the pair of yellow forewing bands in *charitonius* by a broad B + C red band in *hermathenae*, the broader and more rounded shape of the wings (wingspan 80 mm.), the variably developed row of ventral red spots posterior to the discal cell of the hindwing (Text-fig. 136), and the lack of the pearly-brown markings that are at the apex of the *charitonius* hindwing. Some specimens (*vereattus* Stichel 1912:1) have the forewing band smaller, the yellow over the cubitus faint, hindwing bars II and IV dorsally absent and ventrally only discernible by a differentiation of the brown ground color. This shadow effect of the hindwing markings is similar to that demonstrated as the heterozygous condition in *H. melpomene* and *H. erato* (Emsley, 1964) and is presumably the situation in this form too. The precise relationship of Faro, which is the locality for *vereattus*, to the rest of the range of *hermathenae* is not known but it seems likely that it is near the perimeter.

Specific Characters: The male genital valves are a good character (Text-fig. 61), and the female abdominal processes are slender and uniformly curved (Text-fig. 168); also there are androconia on hindwing veins M1, and M2 in addition to the normal compliment on Sc + R1 and Rs (Text-fig. 108).

33. *Heliconius himerus* Hewitson 1867a
Map 20; Text-figs. 62, 102, 135

The forewing shape is broader and more rounded than in most *Heliconius* and the wingspan is about 75 mm. The black ground color has a forewing yellow band in position A (Text-fig. 11) but no costal spot, and on the hindwing there is a red bar in position II (Text-fig. 12) which is only weakly expressed on the ventral surface, a ventral yellow costal streak and a red basal spot complex (Text-fig. 135).

H. himerus seems sympatric with very few other species of *Heliconius,* for it is known by comparitively few specimens from a few localities in southeastern Ecuador and northeastern Peru at altitudes around 1,000 meters.

Specific Characters: Though similar to those of *H. erato* (Text-fig. 60), the male genital valves are characteristic in that the denticles form a slightly flared margin to the tip of the dorsal process (Text-fig. 62); there are androconia on M1, M2, and M3, but not on the membrane around Rs (Text-fig. 102).

34. *Heliconius erato* (Linnaeus 1758:467)
Map 23; Text-figs. 21, 28, 60, 110, 140, 165

This species, together with *H. melpomene,* is remarkable for its diversity in color pattern over its very wide geographic range, for not only are there races characteristic of different areas but at the boundaries of zones which are characterized by contrasting forms it is highly polychromatic. The genetics of some of the color pattern components has been studied by Turner & Crane (1962), Sheppard (1963) and Emsley (1964), and the status of the different forms has already been recorded (Emsley, 1964).

In essence, the situation is that in Central America, central and northern Colombia, eastern, southern and southwestern Brazil and in the valley of the Huallaga River in northeastern Peru, though there are minor characters peculiar to each area, the general pattern is one of a single red forewing band in position A + B on an iridescent blue or matt black ground color, with a yellow bar on both surfaces of the hindwing in position II. In eastern Colombia, Venezuela and Trinidad the appearance is similar but the yellow bar is lacking on both hindwing surfaces, whereas in western Colombia and western Ecuador it is lacking only dorsally. There is a cline of decreasing blueness from a maximum in western Ecuador round the spurs of the Colombian Andes to Panama and through the Guianas to the Amazon basin where the ground color becomes matt black.

In the Amazon basin the characteristic form has the proximal half of the forewing red (= dennis, Text-fig. 5), the hindwing may or may not have a red ray pattern that occurs in several other species (Text-fig. 6), and the forewing band is yellow and composed of a group of spots over positions A-C (Text-fig. 11). The shape of the band grades from a group of discrete spots in the Guianas to a compact yellow rectangle in position C in specimens from the upper tributaries of the Amazon.

Above about 850 meters in the valleys of the eastern Andes, red replaces yellow on the forewing band and each valley has a distinctive band shape that matches the sympatric forms of *H. melpomene* very closely. The details of this mimetic situation have been presented in Emsley (1964).

In the zones that are between areas with stable but different characteristics, such as the Guianas, central Colombia, the eastern Andes and central Bolivia, the populations are polychromatic and show recombinations of characters which are typical of the neighboring zones together with intermediate characters. It is these zones which have been mainly responsible for the period of taxonomic confusion through which both *H. erato* and *H. melpomene* have passed.

Features common to nearly all the forms are the red forewing costal spot, the yellow hindwing streak and red basal spots (Text-fig. 140) which reach maximum expression in southern Brazil *(H. erato phyllis).* The light markings of the head almost always contain some yellow. The wingspan is about 75-80 mm.

Specific Characters: The male genital valves are a good character (Text-fig. 60); there are androconia on the membrane around both Sc + R1 and Rs (Text-fig. 110). Except in specimens from the valleys of the Cauca, Huallaga, Perene and Ucayali Rivers there are always a group of four basal spots which in southern and eastern Brazil are carried out onto the disc (Text-fig. 140); and the female abdominal processes are curved and slender (Text-fig. 165).

35. *Heliconius telesiphe* Doubleday 1847:103
Map 12; Text-figs. 63, 105, 132, 171

Heliconius telesiphe is unusual in that the paired forewing bands in positions A and E (Text-fig. 11) are reddish-pink. There is bar on the hindwing in position II which may be white or yellow, a red costal spot, a yellow and white hindwing costal streak, a group of red basal spots (Text-fig. 132), and diffuse paired pale intervenal gray streaks on the ventral surface of both fore and hindwings. The wings are elongate, with a span of about 80 mm., and the hindwing

has its posterior border scalloped but almost straight (Text-fig. 132).

There is no doubt that it is an upland species, and its range extends along the eastern Andes between 1,000 and 2,600 meters from southern Colombia to central Peru. It is either uncommon or hard to catch, for it is not well represented in museum collections. It is reasonably constant over its whole range except for the color of the hindwing bar which, north of about latitude 4° S., is yellow (*sotericus* Salvin 1871:413) but which to the south is white *(telesiphe).* The apparently mimetic relationship between *Heliconius telesiphe* and the heliconiine *Podotricha telesiphe* is remarkable for not only do they occupy an almost coincident distribution, but they each have two grossly similar allopatric forms. *Podotricha telesiphe telesiphe* (Hewitson 1867b:564) has a white hindwing bar and occurs to the south and *P. t. tithraustes* (Salvin 1871:415) has a yellow bar and occurs to the north of the same dividing line that separates the two forms of *H. telesiphe.* There are no other species of *Heliconius* sympatric with *H. telesiphe* and it is the only species of the genus which is known to exceed an altitude of 1,300 meters, except perhaps *H. cydno* and members of the *H. melpomene timaretus* complex.

There is a dichromatic form (*cretaceus* Neustetter 1916:597) in which the forewing bands are white instead of red.

Specific Characters: The male genital valves (Text-fig. 63) are indistinguishable from those of some of the nearly related species, but the occurrence of androconia on hindwing veins 1A and 2A and M1 is unique (Text-fig. 105); the female abdominal processes are straight (Text-fig. 171).

36. *Heliconius clysonymus* Latreille 1817:128

Map 22; Text-figs. 66, 106, 133, 167

This species has a single yellow forewing band in position A (Text-fig. 11) on a non-iridescent dark brown ground color, with an orange-red bar in position II + III (Text-fig. 12) on the hindwing which shows pink on the ventral surface. There is a red costal spot, a hindwing yellow streak and three basal spots (Text-fig. 133). The ventral ground color is brown with vague paired pale intervenal light streaks on the hindwing and on the apex of the forewing. The wingspan is about 80 mm., but smaller specimens are known (*micrus* Seitz 1913:395) which may be as little as 60 mm.

The typical form, *clysonymus,* extends from Panama through the western side of Colombia as far as Rio Dagua, into the Cauca and Magdalena Valleys, and on the mountain slopes of the eastern side of the eastern Cordilleras as far as Caracas in Venezuela and down to Banos in eastern Ecuador. Though there are no precise data available it seems to be restricted to between 500 and 1,300 meters. From Panama to the known limits of the species in northern Costa Rica the hindwing red bar becomes broader dorsally and more diffuse ventrally (*montanus* Salvin 1871:414). There are no locality records of either *H. clysonymus* or *H. hortense* (No. 37) from Nicaragua so the distribution of the two species (?) seems discontinuous.

Specific Characters: Neither the male genitalia (Text-fig. 66), the hindwing androconia (Text-fig. 106) nor the basal spots (Text-fig. 133) provide diagnostic specific characters, but the complex taken as a whole, together with the female abdominal processes (as Text-fig. 167), will distinguish the species from all others except *H. hortense* from which it may be separated by its smaller and more regular wing shape.

37. *Heliconius hortense* Guérin-Meneville 1829-38:469

Map 22; Text-figs. 65, 107, 134, 167

This species is known only from Mexico, British Honduras, Guatemala and Salvador and is one of the largest *Heliconius,* with a wingspan of about 100 mm. It has an unusually saturniform wing shape with pronounced scallops between the hindwing vein endings, but is in color and pattern similar to *H. clysonymus,* with the exception that the yellow forewing band is centered over the apex of the discal cell midway between positions A and B.

Specific Characters: Neither the male genital valves (Text-fig. 65), the hindwing androconia (Text-fig. 107) nor the basal spots (Text-fig. 134) provide good characters, but taken together with the curved female abdominal processes (Text-fig. 167) they distinguish this species from all others with the exception of *H. clysonymus* from which it may be separated by the larger size and special wing shape.

THE *CHARITONIUS* GROUP

Group features are the absence of signa on the bursa copulatrix (Text-fig. 28), the sparse distribution of androconia only on hindwing veins Sc + R1 and Rs and on the membrane around one or both of them (Text-figs. 109, 111-118), the highly unequal lengths of the paronychial processes (Text-fig. 21), the rounded shape of the male genital valves (Text-figs. 64, 67-74) and the lack of terminal denticles, the presence of conspicuous basal spots (Text-figs. 137-147) and the very squat female abdominal processes as in Text-fig. 172.

38. *Heliconius charitonius*
(Linnaeus 1767:757)
Map 21; Text-figs. 64, 109, 137

This is the most northerly ranging of all the species of *Heliconius,* for in warmer years it reaches California on the west coast of North America and South Carolina on the east, and even in abnormally cold years it can be expected to survive north of the Mexican border and in Florida. The geographic variation in this species has been studied in detail by Comstock & Brown (1950) and barely distinct races have been described from Florida (*tuckeri* Comstock & Brown 1950:15), Mexico (*vazquezae* Comstock & Brown 1950:16), Cuba (*ramsdeni* C. & B. 1950:14), Jamaica (*simulator* Röber 1921:4), Hispaniola (*churchi* C. & B. 1950:14), Puerto Rico and the Virgin Islands (*charitonius*), St. Kitts Antigua and Montserrat (*punctatus* Hall 1936:276), and northern Colombia (*bassleri* C. & B. 1950:16). In southwestern Ecuador and northwestern Peru the form *peruvianus* C. & R. Felder 1859:396 is well differentiated by the distal reduction of the forewing line along Cu1b and the lengths of the forewing bands, which are white, and by the less elongate and more rounded wing shape.

The ground color is a non-iridescent dark brown with a yellow line over the forewing cubitus which is deflexed posteriorly along the anterior margin of Cu 1 b, a pair of oblique yellow bands in positions B and D and a red costal spot. On the hindwing there is a yellow bar in position II, a row of small spots in positions IV and V, and on the ventral surface there is a yellow costal streak, a brown marking at the distal extremity of the bar III position and red basal spots as in Text-fig. 137. The basal spots are visible dorsally and include a pair on hindwing veins 1A and 2A. The wings are elongate and have a span of about 85 mm.

Specific Characters: Neither the male genital valves (Text-fig. 64), the hindwing androconial distribution (Text-fig. 109) nor the female abdominal processes (Text-fig. 172) are diagnostic, but these characters taken with the color pattern and the basal spot complex (Text-fig. 137) are definitive.

39. *Heliconius ricini* (Linnaeus 1758:466)
Map 22; Text-figs. 67, 111, 139

This butterfly, with a wingspan of 65 mm, looks superficially like a small *H. clysonymus,* but the yellow forewing band is more proximal (A), there is a distal yellow band in position D and a yellow line over both surfaces of the cubitus stem. The hindwing has a dorsal bar over coalesced positions I + II + III, a group of basal spots, some of which are expressed dorsally (Text-fig. 139), and a single red spot between the veins 1A and 2A. There is a red costal spot on the forewing, a yellow costal streak on the hindwing and faint paired intervenal white streaks emanating from submarginal white dots.

It is relatively constant throughout its range, which extends from Caracas in Venezuela through the Guianas into the Lower Amazon as far as Ceara on the Brazilian coast. The form *insulanus* Stichel 1909:179 from Venezuela and Trinidad seems to differ from typical *ricini* only in having been caught fresh before the red of the hindwing bar had faded in sunlight. There are no other sympatric species of *Heliconius* with a similar color pattern.

Specific Characters: The male genital valves are relatively small and without special features (Text-fig. 67) and they cannot be distinguished from those of *H. demeter* or *H. sarae.* The hindwing androconia are sparse (Text-fig. 111), the basal spot complex is distinctive (Text-fig. 139) and the color pattern is clearly recognizable.

40. *Heliconius demeter* Staudinger 1896:310
Map 2; Text-figs. 68, 112, 138

This species is known by comparatively few specimens from widely separated localities in the lower-middle Amazon, but such individuals as are known conform to the trends in pattern noticed in all the other dennis-rayed species.

In the Guianas *eueidius* Oberthür 1916:37 (= *egeriformis* Joicey & Kaye 1916:430 = *automatius* Oberthür 1925:81) has a broken yellow band together with dennis (Text-fig. 5) and an *erato*-type ray pattern (Text-fig. 6) which bears dorsally a basal bar in position I. In more western localities the forewing band becomes compact, rectangular and distal to the discal cell (*demeter* = *bouqueti* Nöldner 1901:7).

The minor characters are a yellow forewing costal spot, a yellow hindwing costal streak, three red basal spots (Text-fig. 138), and a ventral single row of paired white submarginal dots. The light head markings are all white and the wingspan is approximately 70 mm.

Specific Characters: The small male genital valves have no distinctive features (Text-fig. 68); the androconia are sparse (Text-fig. 112) but the forewing costal spot is yellow.

41. *Heliconius sarae* (Fabricius 1793:167)
Map 24; Text-figs. 69, 113, 142

Heliconius sarae is a very widely distributed yellow and blue butterfly which, though rela-

tively uniform, has differentiated into recognizable geographic races.

In Central America, and extending into northern Colombia and Venezuela, the typical *sarae* has a pair of yellow forewing bands in positions A and D (Text-fig. 11), the proximal of which is long and narrow, an intervenal white fringe around the posterior border of the hindwing, and one or two red spots on the ventral surface of the hindwing in addition to the group of four basal spots. The forewing costal spot is red as is the comma-shaped hindwing costal streak (Text-fig. 142) and there is a ventral yellow line along the forewing radius. The wingspan is about 70 mm.

In Panama there is a dichromatic form (*theudelus* Hewitson 1874:224) which has a broad yellow cream or white posterior border to the hindwing which is composed of adpressed pairs of short intervenal streaks in position IV. In this form the peripheral white scales are lacking. Throughout Central America there are forms of *sarae* in which the inner forewing band is partly white (*veraepacis* Bates 1864:57).

Where the species extends down the western side of the Andes, the forewing band is shorter and rectangular and the margin of the hindwing in position V is narrowly pure white (*sprucei* Bates 1864:57).

East of the eastern Cordilleras of Colombia and extending widely over the Amazon basin, the long narrow inner band of *sarae* becomes short, broad and oval and the number of postdiscal ventral hindwing spots increases from one or two to four or five (*thamar* (Hübner 1806-19)). Intermediate forewing band conditions occur in the Magdalena Valley, central Colombia and Venezuela (*magdalenae* Bates 1864:57), together with specimens in which the discal band is reduced and divided into a pair of spots (*lilianae* LeMoult), or in which the distal band is absent (*brevimaculatus* Staudinger 1896: 292). Rare specimens are also known from this area in which the forewing spots are ochreous (*aurentiacus*) or white instead of yellow (*albimaculatus* Staudinger 1896:292; *albulus* Riffarth 1900:208). White-banded forms also occur in the Guianas (*albineus* Riffarth 1899).

Around the coast of Brazil the yellow discal forewing band is broad and rectangular (*apseudes* (Hübner 1816:13)) with four to seven postdiscal red ventral hindwing spots (Text-fig. 142), so there is a north-to-south cline in the development of these spots with the maximum of two in Central America rising to five in eastern Colombia and to seven in southeastern Brazil.

It is interesting to notice that the variation in the shape of the forewing band in *sarae* matches, or is matched by, that of the sympatric forms of *H. wallacei*, though it is doubtful if this is of mimetic significance.

Specific Characters: The small male genital valves are without distinctive features (Text-fig. 69), the androconia are concentrated on the veins (Text-fig. 113), the anterior red costal spot is small and rounded (Text-fig. 142) in contrast with that of *H. leucadius*.

42. *Heliconius leucadius* Bates 1862:556

Map 25; Text-figs. 70, 114, 141

This species occurs sympatrically with *H. sarae thamar* over the middle Amazon (and perhaps lower) and along the foothills of the eastern Andes; in appearance it is very similar but it can be separated on the shape of the most anterior basal spot (Text-fig. 141). The typical form *(leucadius)* has a fine intervenal white fringe on the posterior border of the hindwing but there is a dichromatic form which has short coalesced pairs of intervenal white streaks around the hindwing (*pseudorheus* Staudinger 1896:291). The two forms seem fully sympatric. The minor characters are similar to those of *H. sarae* but *H. leucadius* is a little larger (80 mm.).

Specific Characters: The male genital valves (Text-fig. 70) and androconial distribution (Text-fig. 114) hardly contrast with *H. sarae* and reliance has to be placed on the shape of the anterior basal spot which in *H. leucadius* is elongate. Though probably not infallibly, *leucadius* can be distinguished from *sarae* dorsally by the failure of the discal forewing band to cross Cu1b in *leucadius*.

43. *Heliconius hygianus* Hewitson 1867

Map 11; Text-figs. 71, 115, 143

This species is superficially similar to *H. clysonymus* but differs considerably in points of detail. The ground color is dark brown with a narrow discal yellow forewing band in position A and a small rounded yellow band in position E (Text-fig. 11). There is a dorsal and ventral forewing yellow line over the stem of the cubitus, a red forewing costal spot, a red hindwing costal streak enclosed by the recurrent humeral branch of the subcosta, and a group of red basal spots (Text-fig. 143). The hindwing also has a broad dorsal and ventral orange bar in position II, but is without trace of white on the margins of the wings.

H. hygianus is known by a small number of specimens taken from the western Ecuadorian Andes at altitudes between 500 and 1,000 meters.

Specific Characters: The male genital valves (Text-fig. 71) and androconial distribu-

tion are not good characters within the group, so reliance has to be placed on the alary color pattern.

44. *Heliconius antiochus* (Linnaeus 1767:1068)
Map 26; Text-figs. 73, 117, 144

H. antiochus extends from the Magdalena Valley and eastern cordilleras of Colombia through Venezuela, the Guianas and along the Amazon to the 400-meter level of its main tributaries at the foothills of the Andes. Though it could be expected to occur in Trinidad, there are no authentic records of it having done so.

The typical form *(antiochus (Linnaeus* 1767: 1068)) occurs over the whole range of the species except in the Magdalena Valley, though it is uncommon in Venezuela and eastern Colombia. It is a dark, slightly iridescent, blue above, with a pair of entire narrow white forewing bands in positions A and D (Text-fig. 11), a forewing line over both surfaces of the cubitus (though it is absent dorsally in *albus* Riffarth 1900:208) and along the ventral surface of the radius (Text-fig. 3). In the lower Amazon and Guianian areas the inner forewing band may be divided *(zobeide* Butler 1869:18). Commonly in eastern Colombia and always in the Magdalena Valley, the forewing bands are yellow and again either entire *(araneus* (Fabricius 1793:168)) or divided *(ocannensis* Stichel & Riffarth 1905:181).

From a restricted locality on the border between Venezuela and British Guiana, there are a small number of specimens known *(salvinii* Dewitz 1877:86) in which, in addition to the typical characters, there is a broad dorsal and ventral hindwing yellow bar in position II. Some specimens are known from neighboring localities in which there is a faint scattering of yellow scales in the hindwing dorsal bar position and a slight differentiation of the ventral bar area. These may represent a heterozygous yellow bar condition similar to that noticed in *H. erato* and *H. melpomene* from Colombia (Emsley, 1964).

In all specimens the frons is white but the remaining head markings are yellow. The forewing costal spot is composed of scattered red or yellow scales or both, the hindwing costal streak is comma-shaped and red and the basal spots form a complex which is similar to that of *H. sapho* (Text-figs. 144 and 145). Specimens from Colombia are larger (85-90 mm.) than those from the Amazon (75-85 mm.).

Specific Characters: The male genital valves are thickened postero-ventrally (Text-fig. 73), there are no androconia on the membrane around Rs (Text-fig. 117) and the basal spots are as Text-fig. 144, all of which are characters common also to *H. sapho* and *H. hewitsoni*, so specific distinction has to be based on color pattern.

45. *Heliconius sapho* (Drury 1782:54)
Map 25; Text-figs. 72, 116, 145, 147

This species is variable in ground color, forewing band pattern and in the development of the light border to the hindwing. The characters which are reasonably constant include the hindwing red basal spots and red costal streak complex (Text-fig. 145) and red forewing costal spot, so in order to describe the principal forms the characters which undergo modification will be treated separately.

The forewing band and hindwing light border are each independantly modified. From Honduras to Costa Rica the forewing band of *leuce* Doubleday 1847:102 is white and rectangular over positions A to D but with incisions on the anterior and posterior margins and with a distally convex periphery. Between southern Costa Rica and the valleys of northern Colombia, the band becomes more restricted and distally truncate but still entire *(sapho)*. This band type persists polychromatically in northern Colombia with the semidivided band of *eleusinus* Staudinger 1885-88:7, which is itself a transition towards the fully divided double yellow band (positions A and D) of the sympatric *eleuchius* Hewitson 1854. Further south, on the western side of the Andes as far as southwest Ecuador, the double yellow divided band persists alone in *primularis* Butler 1869:18. The form *deflavus* Joicey & Kaye 1917:93 is an aberration of *primularis* in which the hindwing border is very faint. The form *ceres* Oberthür 1920a:30 has not been seen but it is probably a minor variation of *eleusinus*.

The hindwing border is narrow and white in position V from Honduras to Costa Rica *(leuce)*, but broadens in *sapho* from Costa Rica and Panama to the very broad white border of *eleuchius* (positions IV + V). The narrow border seen in *leuce* persists in Panama and northern Colombia in *eleusinus* but the only form known from western Colombia and western Ecuador is the very broad yellow and/or white border of *primularis* in positions III + IV + V.

On the eastern side of the Andes between central Colombia and northern Peru, *congener* Weymer 1890b:117 has a pair of yellow forewing bands (positions A and D) and a medium blue iridescent ground color without any hindwing border except white intervenal fringing scales. The anterior red basal spot is smaller than in typical *sapho* (Text-figs. 145, 147).

Specific Characters: The male genital

valves are thickened postero-ventrally (Text-fig. 72), there are no androconia around Rs (Text-fig. 116) and the basal spots are as Text-fig. 145, but as none of these characters differentiates this species from either *H. antiochus* or *H. hewitsoni,* reliance has to be placed on color pattern.

46. *Heliconius hewitsoni* Staudinger 1875:98
Map 10; Text-figs. 74, 118, 146

This butterfly is exceptionally similar to *H. pachinus* with which it is sympatric. It has a pair of yellow forewing bands in positions A and E on a scarcely iridescent dark blue ground color, and has a broad yellow bar on the hindwing in position IV. The dorsal pattern is expressed ventrally together with a yellow forewing line along the radius, a red costal spot, a comma-shaped red costal streak on the hindwing and a group of red basal spots (Text-fig. 146).

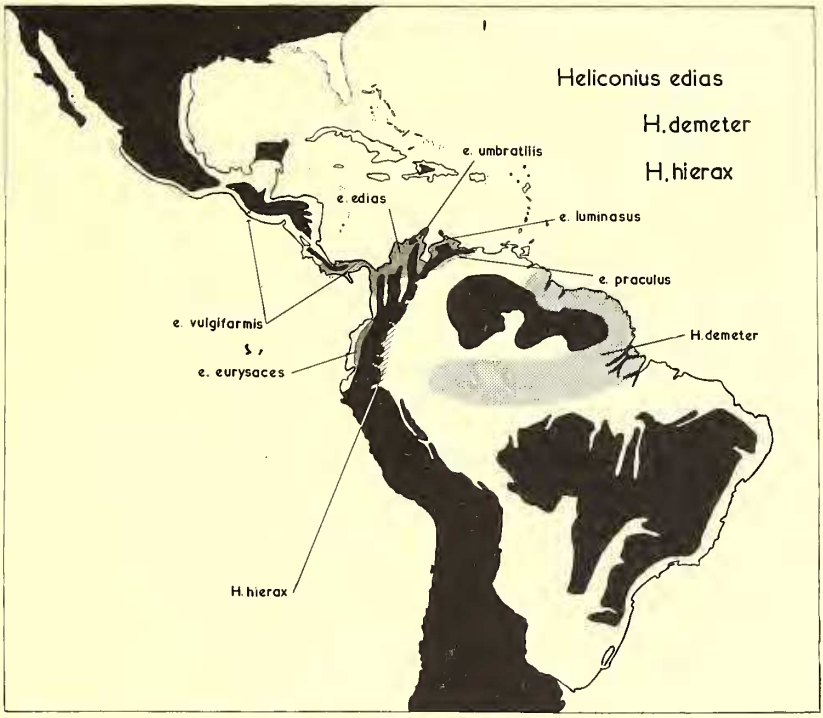
The localities from which *hewitsoni* are known are Sevilla Island, Parida Island, Chiriqui Volcano, Bugaba, Lino (which are all in Panama) and Pozoazul and other unspecified localities in Costa Rica. It has been suggested by Seitz (1913) and others that this is a high altitude form of *H. sapho* but the data do not support this view.

Specific Characters: The male genital valves have a postero-ventral thickening (Text-fig. 74), there are no androconia on the membrane around Rs (Text-fig. 118), the basal spots are as in Text-fig. 146, but none of these characters are diagnostic, so reliance has to be placed on color pattern. It may be distinguished from *H. pachinus* by the more precise boundaries and proximal position of the forewing bands, and by the more elongate shape of the basal spot in the angle between Sc + R1 and Rs (Text-figs. 146 and 128). All the basal spots in *pachinus* have more diffuse edges then in *hewitsoni.*

NOTE ON MAPS

On the 26 maps that follow, the black areas are where no *Heliconius* are known to occur, as judged by museum specimens. It seems likely that the distribution of *Heliconius* is more extensive along the river valleys of the Brazilian highlands than is shown on the maps.

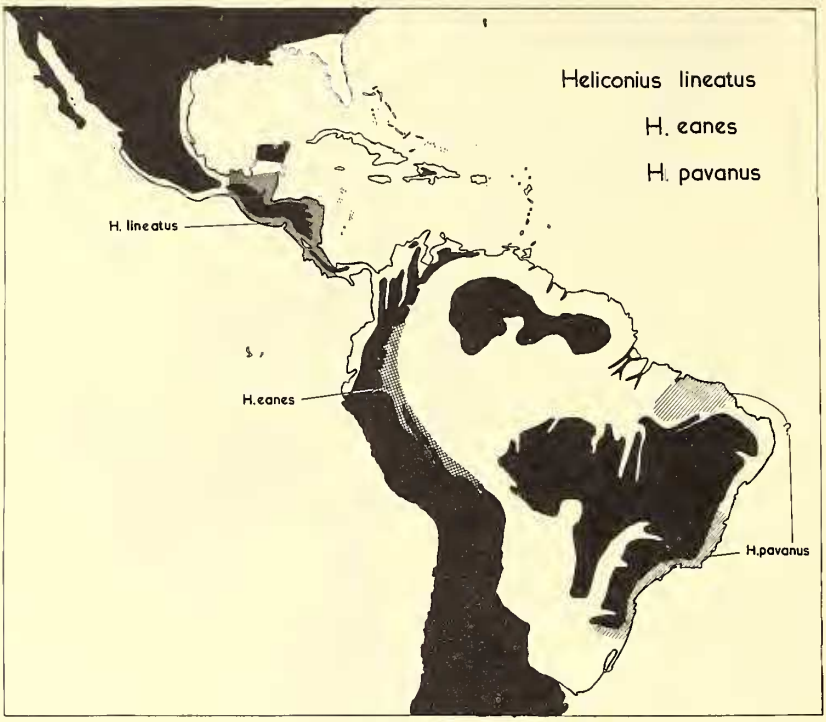
Map 1


Heliconius edias
H.demeter
H.hierax
e. umbratilis
e. edias
e. luminasus
e. praculus
e. vulgifarmis
♀
e. eurysaces
H.demeter
H.hierax

MAP 2


Heliconius vibilius
new form ?
unifasciatus
?
?
vialis
♀
vibilius
lampeta etc.

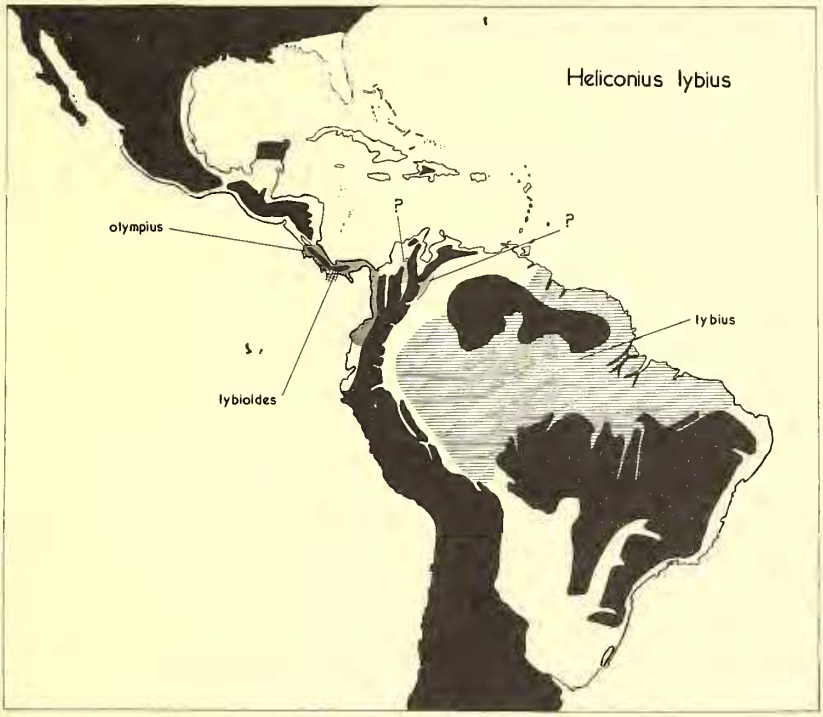
MAP 3


Heliconius lineatus
H. eanes
H. pavanus
H. lineatus
H.eanes
H.pavanus

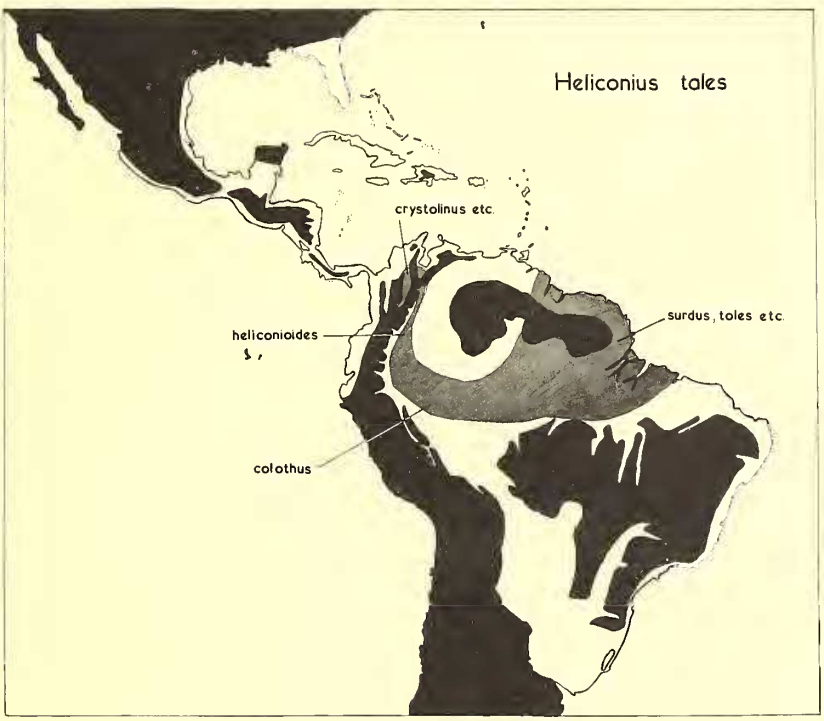
MAP 4


Heliconius isabellae
cleobaeus
manachramus
zarcaan
isabellae
hippolinus etc.
dianasus

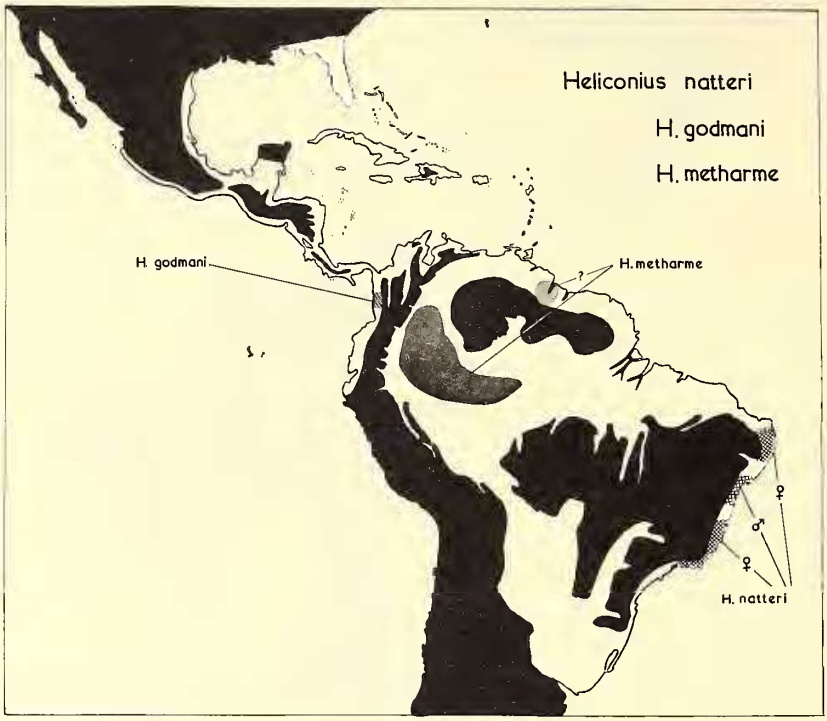
MAP 5


Heliconius lybius
olympius
P
P
lybius
lybioides

MAP 6


Heliconius tales
crystolinus etc.
surdus, toles etc.
heliconioides
colothus

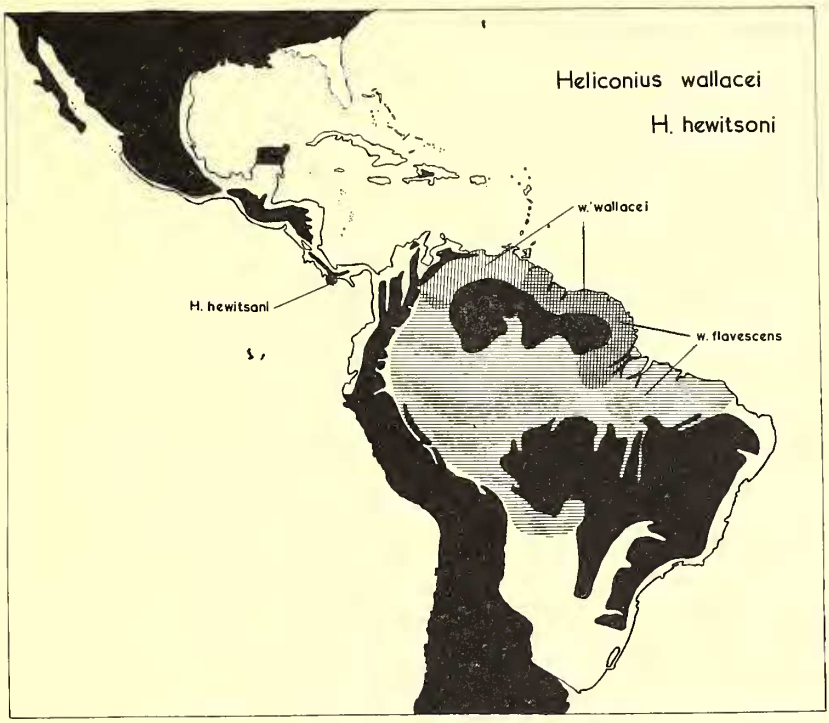
MAP 7


Heliconius natteri
H. godmani
H. metharme
H. godmani
H. metharme
♀
♂
♀
H. natteri

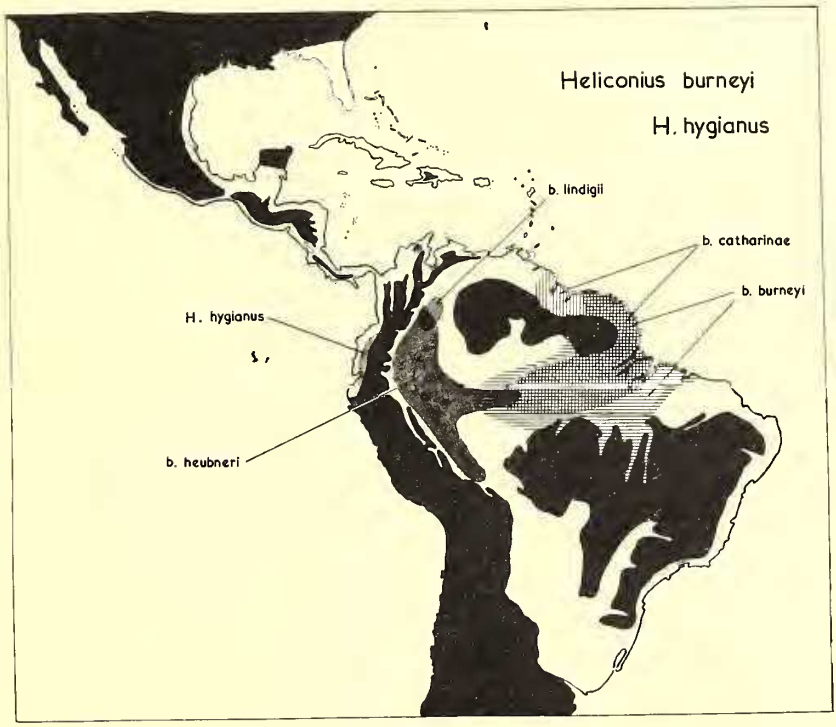
MAP 8


Heliconius aoede
aoede &
astydamius
bartletti & lucretius
cupidineus

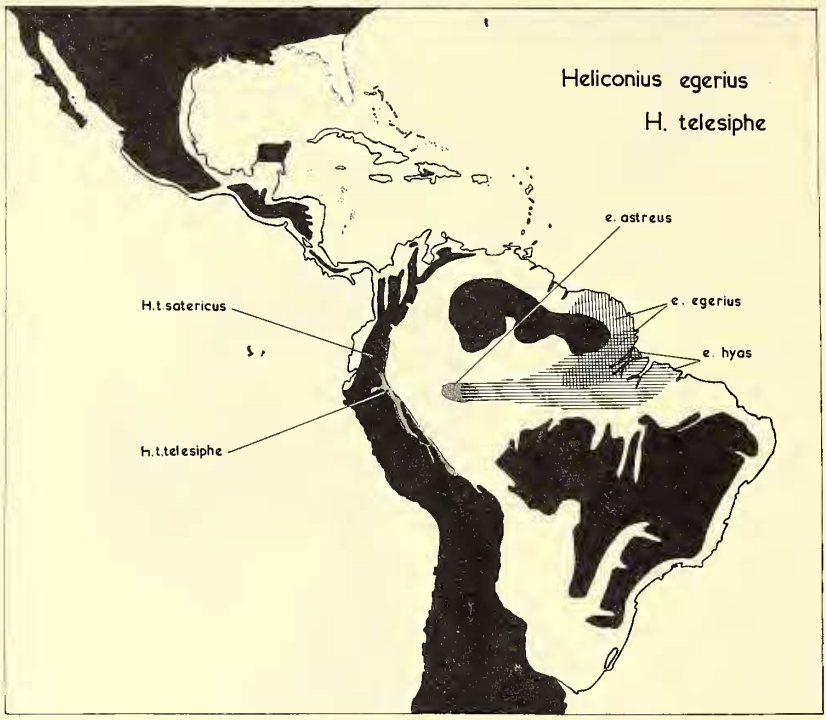
MAP 9


Heliconius wallacei
H. hewitsoni
w. wallacei
H. hewitsani
w. flavescens

MAP 10


Heliconius burneyi
H. hygianus
b. lindigii
b. catharinae
b. burneyi
H. hygianus
b. heubneri

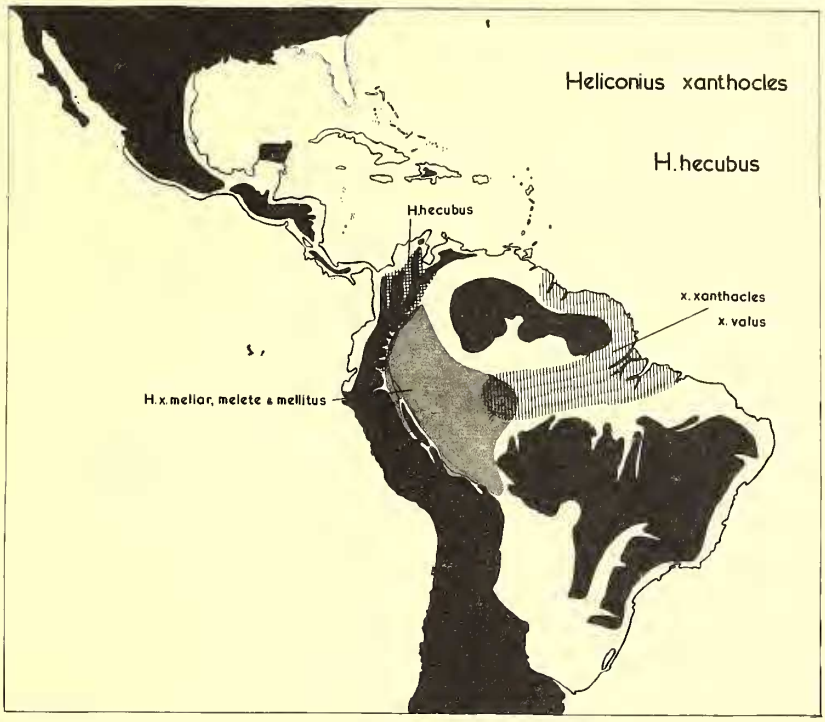
MAP 11


Heliconius egerius
H. telesiphe
e. astreus
e. egerius
e. hyas
H.t.satericus
H.t.telesiphe

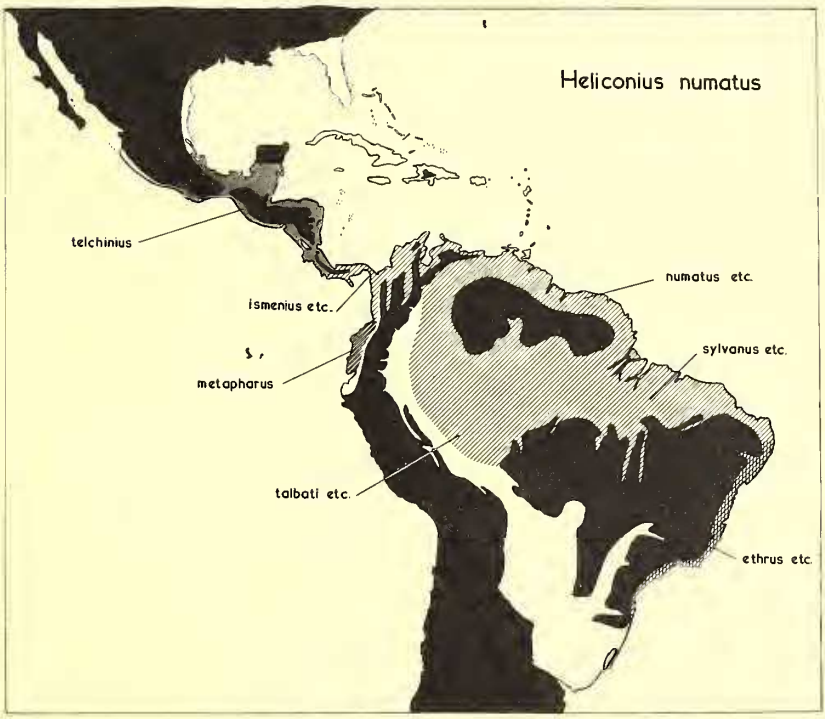
MAP 12


Heliconius doris
viridis etc.
eratanius
delilae
aristamache, doris

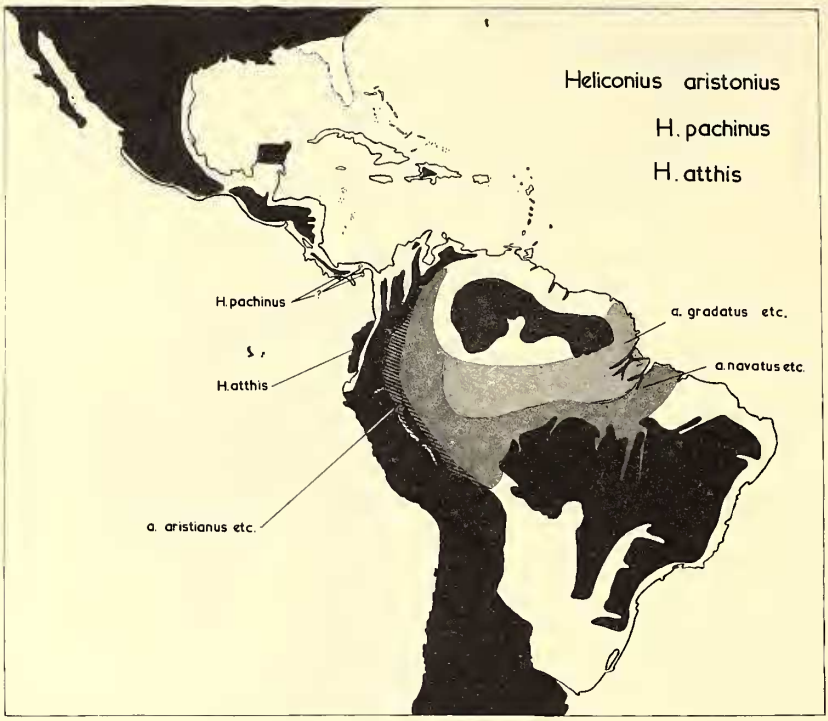
MAP 13


Heliconius xanthocles
H. hecubus
H.hecubus
x. xanthocles
x. vatus
H. x. melior, melete & mellitus

MAP 14


Heliconius numatus
telchinius
ismenius etc.
metapharus
numatus etc.
sylvanus etc.
talbati etc.
ethrus etc.

MAP 15


Heliconius aristonius
H. pachinus
H. atthis
H.pachinus
♀ ,
H.atthis
a. aristianus etc.
a. gradatus etc.
a. navatus etc.

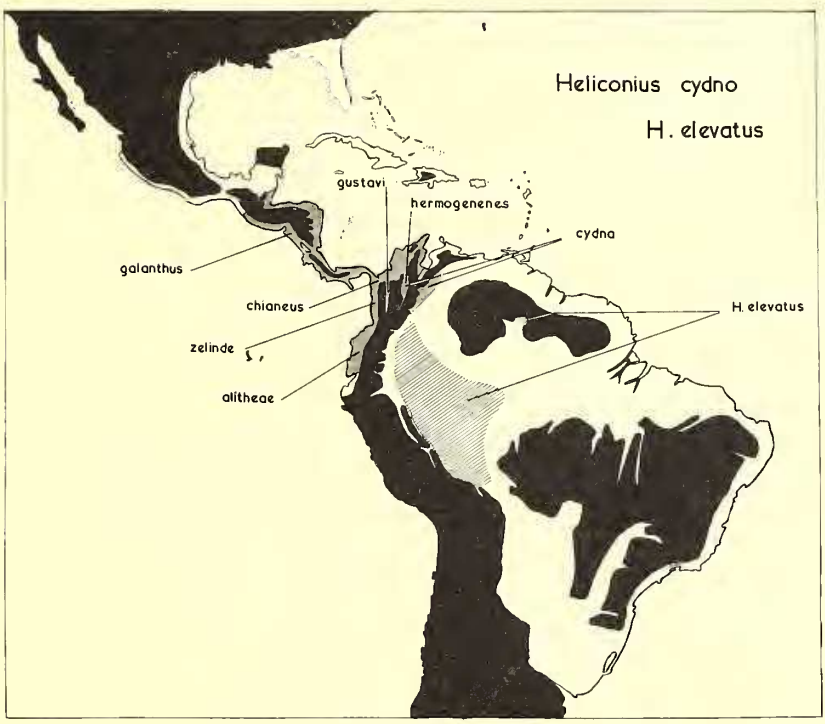
MAP 16


Heliconius ethillus
farnarinus
zuleikus
melicertus etc.
♀ ,
Ithacus etc.
metalilis, ethillus etc.
eucamus etc.
fortunatus etc.
narceus etc.

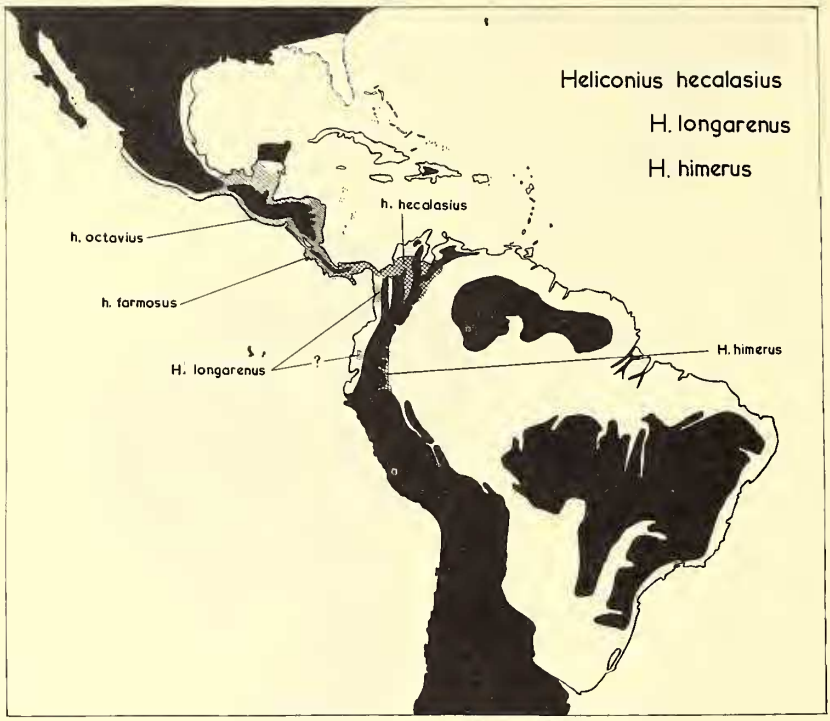
MAP 17


Heliconius melpomene
euryas
heurippus
melpamene
rasinus
vulcanus
thelxiope etc.
cytherus
timaretus etc.
plesseni
ecuadarensis
amaryllis
xenacleus
euryades
besckei
nannus
?

MAP 18


Heliconius cydno
H. elevatus
gustavi
hermogenenes
cydna
galanthus
chianeus
H. elevatus
zelinde
alitheae

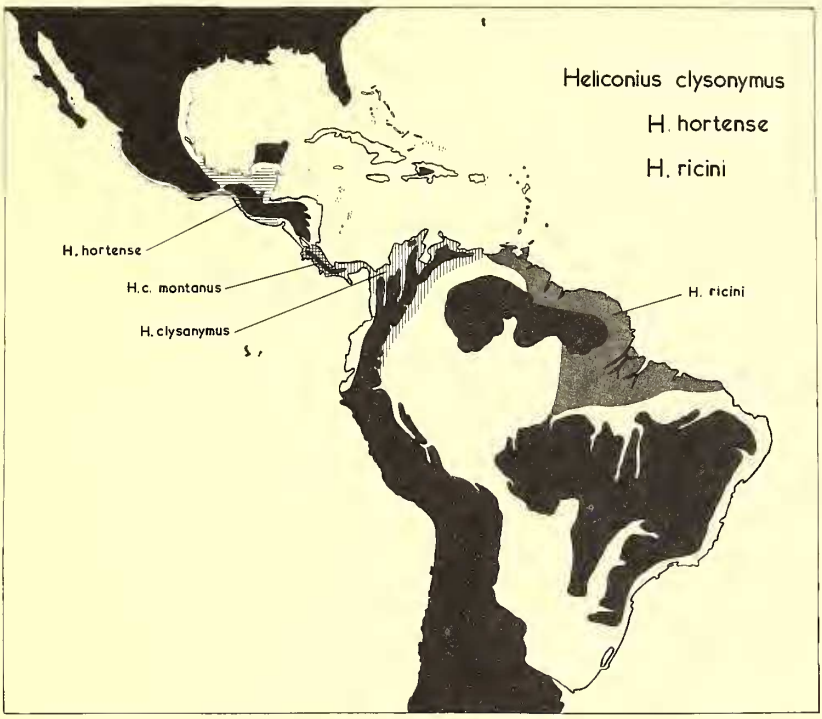
MAP 19


Heliconius hecalasius
H. longarenus
H. himerus
h. hecalasius
h. octavius
h. farmosus
H. longarenus
H. himerus

MAP 20


c.tuckeri
Heliconius charitonius
H. hermathenae
H. hecale
c.ramsdeni
c.churchi
c. punctatus
c.simulator
c. charitonius
c.vazquezae
H.hecale
c.bassleri
H.hermathenae
c.peruvianus

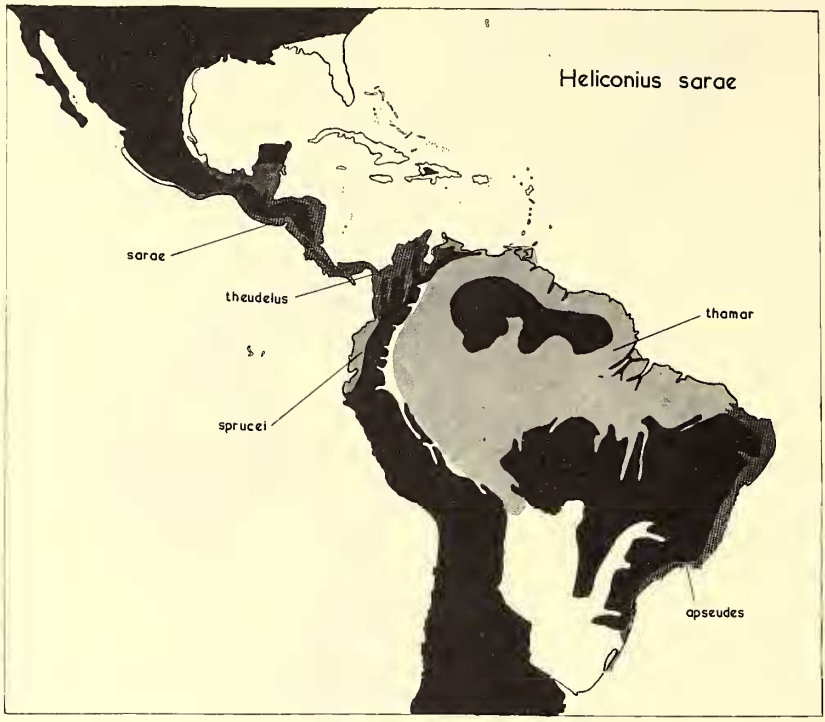
MAP 21


Heliconius clysonymus
H. hortense
H. ricini
H. hortense
H.c. montanus
H. clysanymus
H. ricini

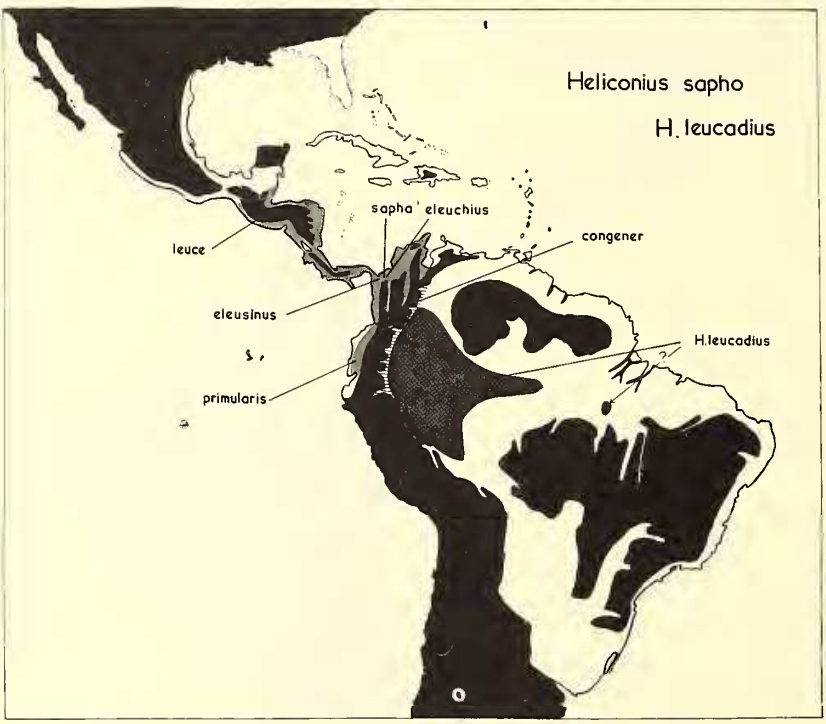
MAP 22


Heliconius erato
chestertoni
calombinus
odonus
petiveranus
venus
erota
cyrbius
notabilis
etylus
favorinus
microcleus
amphitrite
phyllis

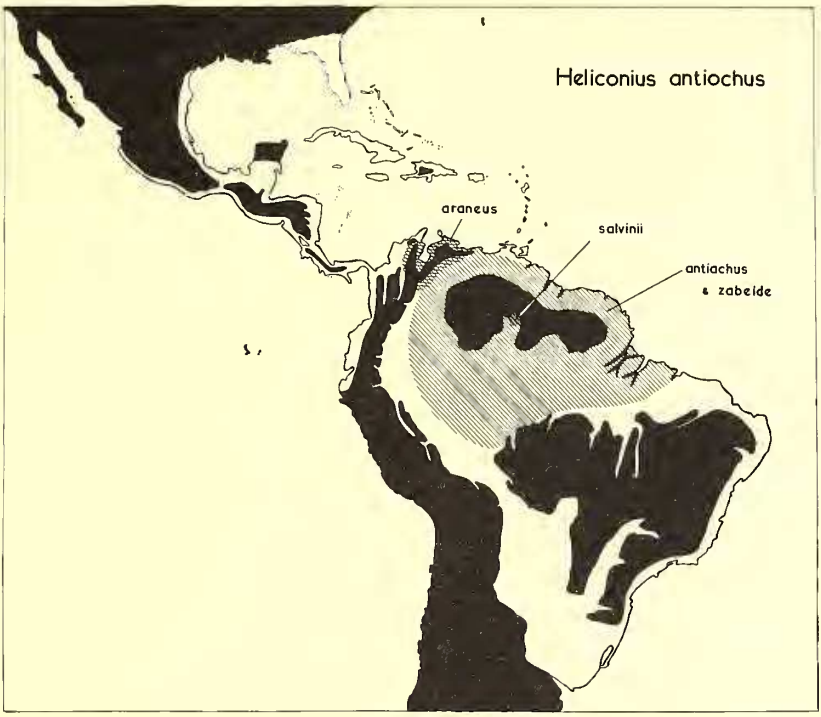
MAP 23


Heliconius sarae
sarae
theudelus
thamar
sprucei
apseudes

MAP 24


Heliconius sapho
H. leucadius
sapha' eleuchius
congener
leuce
eleusinus
H.leucadius
primularis

MAP 25



MAP 26

TAXONOMIC REFERENCES

APOLINAR, M.
1926. Bot Soc. colomb. Ci. nat. Bogota, *15*.
1927. Bot. Soc. colomb. Ci. nat. Bogota, *16*.

BATES, H. W.
1862. Trans. Linn. Soc. Lond., *23*.
1863. Proc. zool. Soc. Lond.
1864. Entomologist's mon. Mag., *1*.
1866. Entomologist's mon. Mag., *3*.
1867. Trans. R. ent. Soc. Lond., (3), *5*.

BILLBERG, ?
1820. Enum. Ins. in Mus. Billberg.

BOISDUVAL, J. A.
1870. Consid. Lép. Guatemala. Rennes.

BOISDUVAL, J. A. & LECONTE, J. E.
1836. Hist. gen. Lép. Chen. Amer., Sept.

BOULLET, E. & LECERF, F.
1909. Bull. Mus. Paris., *15*.
1910. Bull. Mus. Paris., *16*.

BRYK, F.
1953. Ark. zoo. (n. ser.), *5*, Stockholm.

BUTLER, A. G.
1869. Ann. Mag. nat. Hist., (4), *3*.
1873. Cistula Ent., *7*.
1875. Ann. Mag. nat. Hist., (4), *15*.

BUTLER, A. G. & DRUCE, H.
1872. Entomologist's mon. Mag., *9*.

CLERK, ?
1764. Icones, sect. 2.

COMSTOCK, W. P. & BROWN, F. M.
1950. Am. Mus. Novit., No. 1467.

CRAMER, P.
1775-76. Pap. exot., *1*.
1777. Pap. exot., *2*.
1779. Pap. exot., *3*.
1780-82. Pap. exot., *4*.

DEWITZ, H.
1877. Mt. Münch ent. Ver., *1*.

DOUBLEDAY, E.
1847-48. Gen. diurn. Lep., *1*.

DRUCE, H.
1874. Trans. R. ent. Soc. Lond.
1876. Proc. zool. Soc. Lond.

DRURY, ?
1782. Nat. Hist., *3*.

ERICHSON, ?
1848. Schomburgk, Guiana, *3*.

FABRICIUS, J. C.
1775a. Gen. Ins.
1775b. Syst. Ent.
1793. Syst. Ent., *3*.

FASSL, A. H.
1912. Ent. Rdsch., *29*.

Felder, C. & R.
1859. Wein. Ent. Monatschr., *3*.
1861. Wein. Ent. Monatschr., *5*.
1862. Wein. Ent. Monatschr., *6*.
1865. Reise Novara, *2*.

Fruhstorfer, H.
1910. Ent. Z. Stuttgart.

Geyer, ?
1832. Zutr. exot. Schmett., *4*.

Godart, J. B.
1819. Enc. méth., *9*.

Godman, F. D. & Salvin, O.
1881. Biol. Centr. Amer., Lep. Rhop., *1*.

Goeze, ?
1779. Ent. Beytr., *3*.

Grose Smith & Kirby, W. F.
1892. Rhop. Exot., *1*.

Guérin-Méneville
1829-38. Iconogr. Régn., *3*, Ins.

Hall, A.
1921. Entomologist, *54*.
1930. Entomologist, *63*.
1936. Entomologist, *69*.

Hemming, F.
1933. Entomologist, *66*.

Hewitson, W. C.
1852-54. Exot. Butt., *1*.
1857. Exot. Butt., *2*.
1861. Int. exot., *1*.
1863. Proc. zool. Soc. Lond.
1864. Trans. R. ent. Soc. Lond., (3), *2*.
1867a. Exot. Butt., *4*.
1867b. Trans. R. ent. Soc. Lond., (3), *5*.
1869a. Trans. R. ent. Soc. Lond., (3), *7*.
1869b. Equat. Lep.
1872. Entomologist's mon. Mag., *9*.
1873. Exot. Butt., *5*.
1874. Entomologist's mon. Mag., *10*.
1875. Entomologist's mon. Mag., *11*.

Hayward, K. J.
1931. Rev. Soc. ent. Argent., *4*.
1952. Acta zool. Lilloana, *10*.

Hoffman, C. C.
1940. Ann. Inst. Biol. México, *11*.

Hübner, J.
1806-19. Exot. Schmett., *1*.
1816-19. Verz. bekannt. Schmett.
1825. Samml. Exot. Schmett., *2*.

Joicey, J. J. & Kaye, W. T.
1916. Trans. R. ent. Soc. Lond.
1917. Ann. Mag. nat. Hist., (8), *20*.

Joicey, J. J. & Talbot, G.
1925. Ann. Mag. nat. Hist., (9), *16*.

Kaye, W. J.
1906. Entomologist, *39*.
1913. Proc. R. ent. Soc. Lond.
1916a. Entomologist's Rec. J. Var., *28*.
1916b. Entomologist, *49*.
1919. Ann. Mag. nat. Hist., (8), *3*.

Kluk, ?
1802. Zwierz. Hist. nat. Pocz. Gospod., *4*.

Kotsch, H.
1936. Ent. Rdsch., *53*.

Kruger, R.
1925. Dt. ent. Z., *39*.
1933. Int. ent. Z., *27*.

Kirby, W. F.
1900. Exot. Schmett Hübner.

Lathy, P. I.
1906. Proc. zool. Soc. Lond.

Latreille, ?
1817. *in:* Humbolt and Bonpland, Voy. Amér. *2*.

Lichy, R.
1960. Rev. Fac. Agron. Univ. cent. Venez., *2*, (3). Maracay.

Linnaeus, C.
1758. Syst. nat., ed. 10.
1767. Syst. nat., ed. 12.
1771. Mant. Plant., II.

Ménétriés, ?
1857. Lep. Ac. St. Petersb., *2*.

Michael, O.
1926. Ent. z. Frankfurt., *39*.

Neustetter, H.
1907. Verh. zool.-bot. Ges. Wien.
1908. Verh. zool.-bot. Ges. Wien.
1912. Fauna exot., *2*.
1913. Verh. zool.-bot. Ges. Wien.
1916. *in:* Seitz, Grobschmett., *5*.
1924. Trans. R. ent. Soc. Lond.
1925. Öst. Ent. Ver., *10*.
1928. Int. ent. Z., *22*.
1929. *in:* Strand, Lepidopterorum Catalogus, (36).
1931. Int. ent. Z., *25*.
1932. Öst. Ent. Ver., *17*.
1938. Ent. Rdsch., *55*.

Niepelt, W.
1923. Int. ent. Z., *17*.

Nölder, ?
1901. Berl. ent. Z., *46*.

Oberthür, C.
1902. Études d' Ent., *21*.
1916. Et. Lep. Comp., *12*.
1920. Et. Lep. Comp., *17*.
1923. Et. Lep. Comp., *20*.
1925. Et. Lep. Comp., *22*.

Paclt, J.
1955. Beitr. ent., *5*.

Reakirt, T.
1866. Acad. nat. Sci. Philad.

Riffarth, H.
1899. Berl. ent. Z., *44*.
1900. Berl. ent. Z., *45*.
1901. Berl. ent. Z., *46*.
1906. Insektenbörse, Leipzig, *23*.
1907. Dt. ent. Z.
1908. Berl. ent. Z., *53*.

RÖBER, J.
1923. Ent. mitt., *12*, Berlin.
1927. Int. ent. Z., *21*.

SALVIN,O.
1871. Ann. Mag. nat. Hist., (4), 7.

SALVIN, O. & GODMAN, F. D.
1868. Ann. Mag. nat. Hist., (4), *2*.
1877. Proc. zool. Soc. Lond.

SEITZ, A.
1913. Grobschmett, *5*.
1916. Grobschmett, with appendix, *5*.

SRNKA, A.
1885. Berl. ent. Z., *29*.

STAUDINGER, O.
1875. Verh. zool.-bot. Ges. Wien., *25*.
1876. Verh. zool.-bot. Ges. Wien., *25*.
1882. Proc. zool. Soc. Lond.
1885-88. Exot. Schmett., *1*.
1896. Dt. ent. Z., Lep., *9*.
1900. Dt. ent. Z., Lep., *12*.

STICHEL, H.
1903. Berl. ent. Z., *48*.
1906. Gen. Ins., Wytsman, *37*.
1907. Gen. Ins., fasc. 63, Wytsman.
1909. Societas ent., *23*.
1912. Int. ent. Z.
1919a. Zeit. f. wiss. Ins. Biolog.
1919b. Neue Beiträge zur Syst. Insektenk., *1*.
1923. Dt. ent. Z.

STICHEL, H. & RIFFARTH, H.
1905. Das Tierreich, Heliconiidae, *22*.

STRAND, E.
1912. Archiv. f. Naturgesch.

SWAINSON, W.
1827. Phil. Mag. (n. ser.), *1*.

TALBOT, G.
1932. Bull. Hill Mus., *4*.

WEYMER, G.
1875. Stettin ent. Ztg., *36*.
1884. Stettin ent. Ztg., *45*.
1890a. Stettin ent. Ztg., *51*.
1890b. Lep. Reise Stübel.
1893. Dt. ent. Z., Lep. *6*.
1896. Dt. ent. Z., Lep. *9*.
1906. Dt. ent. Z., Lep. *19*.
1912. Ent. Rdsch., *29*.

ZIKÁN, J. F.
1937. Ent. Rdsch., *54*.

IV. Summary of Evidence for the Systematic Presentation

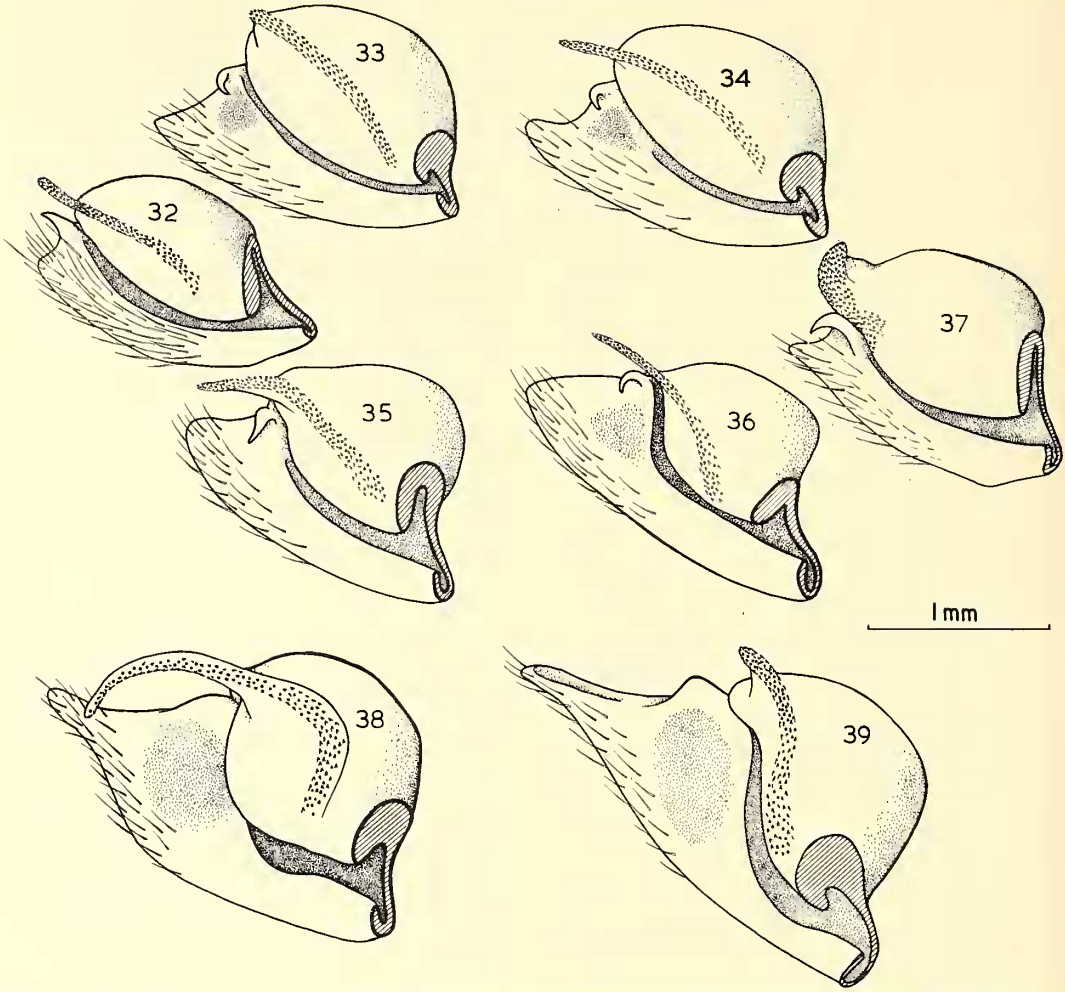
Previous studies on the subfamily have revealed (Emsley, 1963) that there are a considerable number of morphological characters of value in establishing systematic relationships, but concern was then principally with different genera, each containing only a small number of clearly defined species. Though the anatomy of the imagines has been completely re-examined, the only new characters that have been found to be of use are the minor components of the alary color-pattern. The major components of the color-pattern have been avoided as far as possible to guard against misjudgement over convergent similarities due to Batesian or Müllerian mimicry. The relatively inconspicuous features like the forewing costal spot, the hindwing costal streak and the basal spot complex are less likely to have been influenced by such effects or at least have remained more conservative and hence of greater value to the systematist.

The definition of Heliconiinae is reassuringly clearcut, for no other Papilionoidea have the recurrent humeral branch of the hindwing subcosta unforked (Text-fig. 2), have androconia on the wing veins of males and have capitate processes developed from the posterior margin of the eighth abdominal segment of females (Text-figs. 161-172).

Unfortunately, few criteria have been found which will enable the genus to be divided into larger units than the thirteen species-groups proposed here. The shape of the duct from the spermathecal diverticulum (Text-fig. 18) and the reduced number of female protarsal articles (Text-fig. 14) separates the genus into the subgenera *Eueides* and *Heliconius*. Within *Eueides* occur typical *Heliconius* characters like the development of the red basal spots (*H. lybius lybius*) and the presence of androconia on the membrane around Sc + R1 and Rs (*H. tales, H. lybius*) which lessen the clarity of the taxonomic division.

The evidence for the assertion that the *Eueides* species are the more primitive is based on the exclusive restriction of the androconia to the veins of the wings and on the narrowness of the duct from the spermathecal diverticulum, both characters which are common to all the other genera of Heliconiinae. Corroborating evidence is the acute angle through which the signa of the bursa copulatrix are curved, which is again a heliconiine character. Less convincing but worth noting is the occurrence of a denticulate zone along the interior surface of the dorsal portion of the male genital valve in all *Eueides* species (Text-figs. 32-39), in most of the other genera but in few of the subgenus *Heliconius* (Text-figs. 40-74) (on other criteria those species of *Heliconius* which have this extensive denticulate zone are considered among the most primitive).

The unity of *Eueides* is supported by a tendancy to asymmetry in the signa which is at its maximum in *H. alipherus* (Text-figs. 24, 25), is strong in *H. tales* (Text-figs. 153, 154) and *H. lybius* (Text-figs. 151, 152) and is detectable

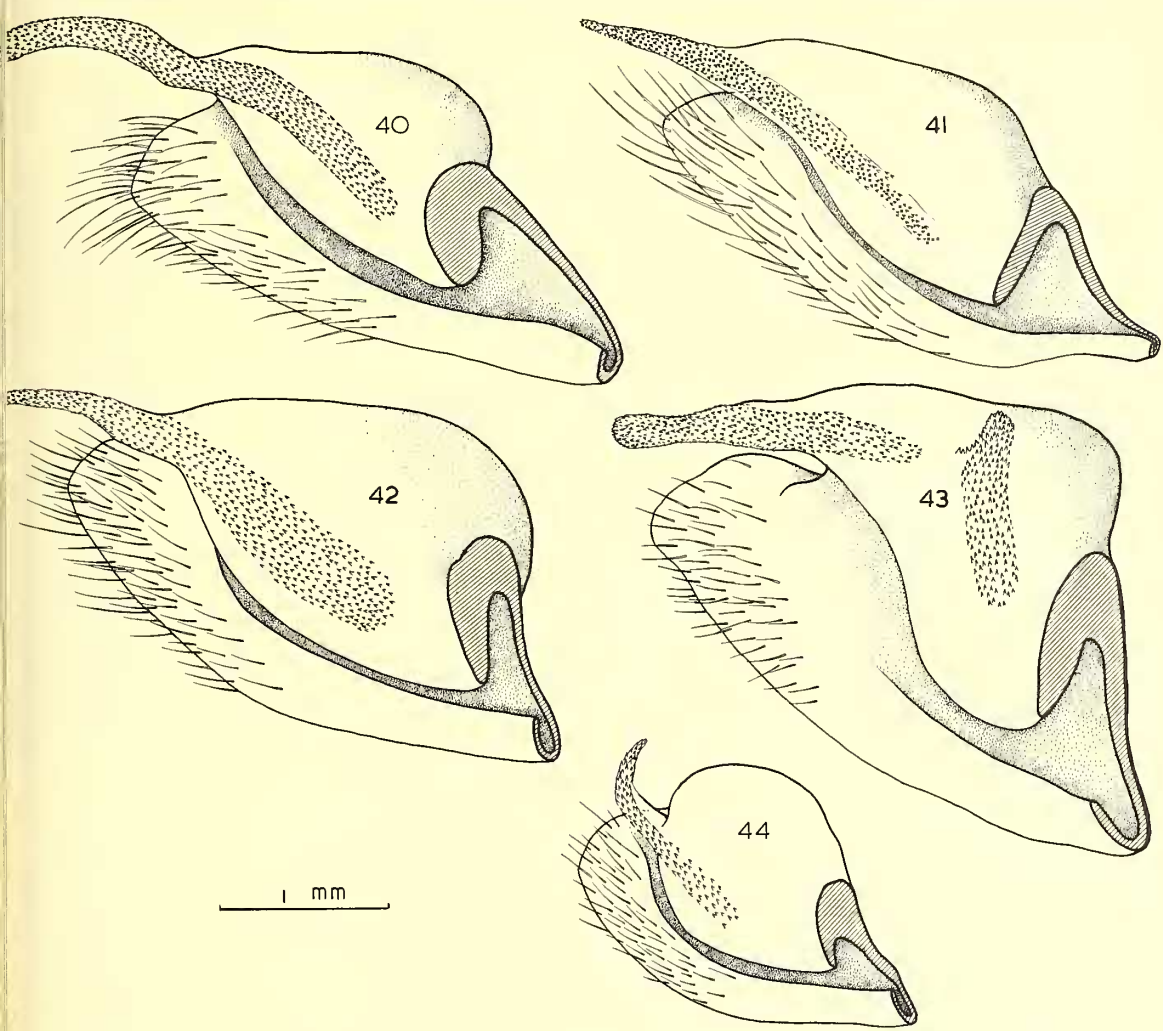


TEXT-FIGS. 32-39. Inner aspect of left genital valves of male *Heliconius*. **32,** *H. alipherus;* **33,** *H. vibilius* or *H. pavanus;* **34,** *H. edias;* **35,** *H. lineatus;* **36,** *H. eanes;* **37,** *H. isabellae;* **38,** *H. lybius;* **39,** *H. tales.*

throughout the subgenus. There is also a tendancy for the pretarsal paronychia to be more coarsely spinose and more broad apically than in the subgenus *Heliconius* (Text-figs. 19-23).

The similarity between *H. alipherus* and *Colaenis iulia,* both in the hand and in flight, is most striking and, in view of the correlated variation in their appearance in the northwestern part of their grossly similar and extensive range, it is tempting to postulate a mimetic association. However, the occurrence of a similar pattern in *H. lybius* and *H. lineatus* allows the possibility that the pattern is a relic. In fact, it is not difficult to imagine the derivation of the patterns seen in *H. natteri, H. hecalasius, H. longarenus* and *H. vibilius* from that of such an ancestor. The red basal spots, which are highly developed in some species of *Heliconius,* and are present in most, are present also in *Colaenis iulia, Agraulis vanillae* and in an orange form in *Philaethria dido,* so these too may be an ancestral character.

The evolutionary scheme presented here has been based on the premise that the presence of androconia on many fore or hindwing veins is a primitive character. This premise has been accepted because *Philaethria, Dione* and *Podotricha* have androconia on nearly all the fore and hindwing veins, *Agraulis* and *Dryadula* have them on many hindwing veins and in *Colaenis* they are present on up to six forewing veins and on hindwing veins Sc + R1 and Rs, as in all *Heliconius.* If the discal cell of *Colaenis* was closed by the cross-vein M2-M3, then the only character which would be inconsistent with it being



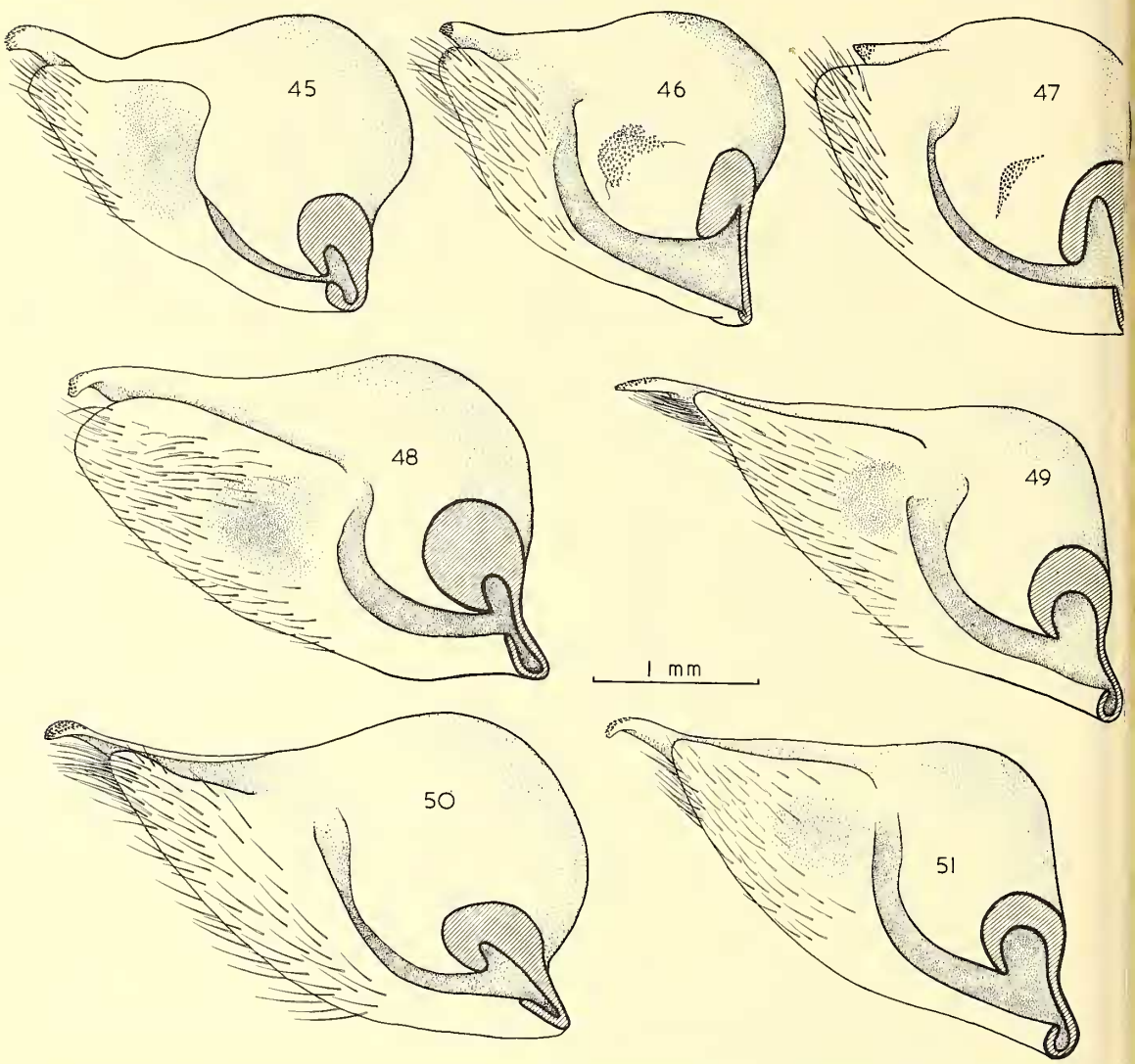
TEXT-FIGS. 40-44. Inner aspect of left genital valves of male *Heliconius*. **40**, *H. egerius egerius;* **41**, *H. wallacei;* **42**, *H. burneyi;* **43**, *H. egerius astreus;* **44**, *H. hierax.*

placed in *Heliconius (Eueides)* would be the five-articled female foretarsus.

Within *Eueides, H. alipherus* and *H. edias* seem the most primitive on account of their more extensive androconial distribution (forewing *H. edias,* Text-fig. 98; hindwing *H. alipherus,* Text-fig. 75). The signa of both these species are broader than any other in *Heliconius* and similar to that of *Philaethria* (Text-figs. 24, 25, 149 and in Emsley 1963: fig. 124).

The male genital valves of *H. vibilius, pavanus, eanes* and *lineatus* are very like those of *H. edias* (Text-figs. 33-36), but the androconial distribution is restricted to the hindwing veins Sc + R1 and Rs (Text-figs. 76-77) and the signa are more arcuate (Text-fig. 150). Straightness is considered a primitive characteristic of the female abdominal processes, so no great importance is attached to this similarity in these species.

H. isabellae differs from the other members of the *vibilius* group principally in the male genital valves (Text-fig. 37) and in the details of the androconial distribution (Text-fig. 78), so it is deemed to be included. The male genitalia of this group are not very different from those of *H. alipherus* (Text-fig. 32) but on androconial distribution and asymmetry of the signa they must remain distinct. No particular importance is attached to the loss of the terminal spine on the female foretarsus in *H. alipherus* (Text-fig. 15) and *H. pavanus* as gross reduction of the foretarsus is a feature of *Eueides.* A similar reduction was noticed in *Dione* and *Agraulis* (Emsley 1963:106). The reduction of the signa in *pava-*



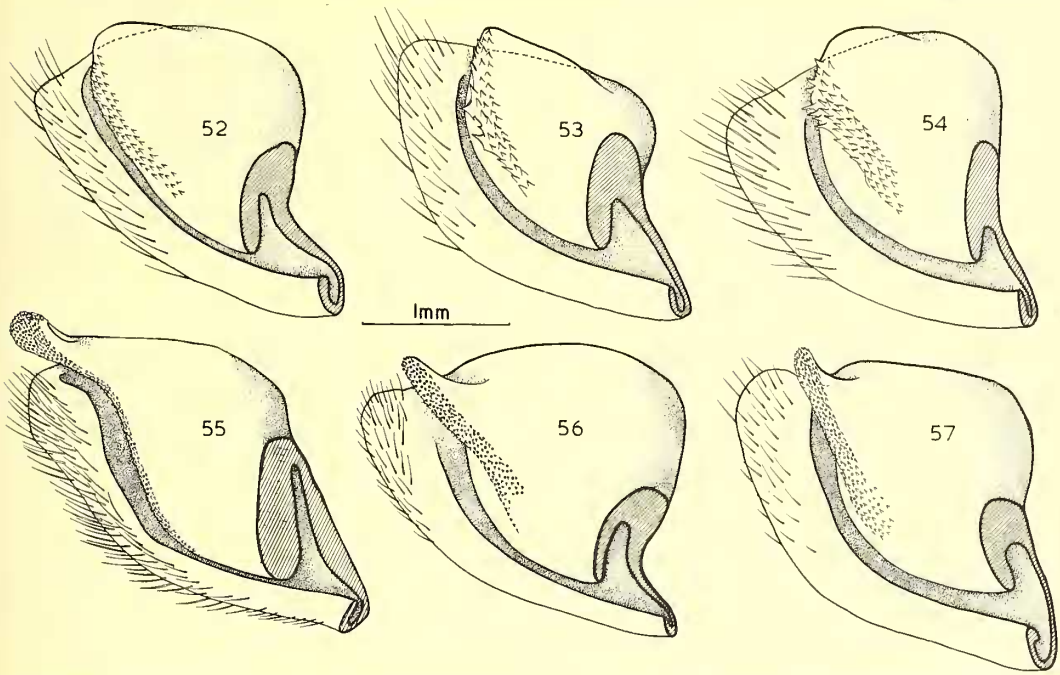
TEXT-FIGS. 45-51. Inner aspects of left genital valves of male *Heliconius*. **45,** *H. natteri;* **46,** *H. melpomene;* **47,** *H. cydno;* **48,** *H. numatus;* **49,** *H. ethillus* or *H. elevatus;* **50,** *H. atthis;* **51,** *H. aristionus.*

nus (Text-fig. 148) is considered to be a specialization and perhaps illustrates the mode of loss in some of the higher groups.

The two species *H. tales* and *lybius* have similar but distinctive genital valves (Text-figs. 38, 39) and are distinguished from all other *Eueides* by the presence of androconia on the membrane around the veins Sc + R1 and Rs. Their signa are also more acute-angled and more slender than any other species in the genus (Text-figs. 151-154), and their female abdominal processes are strongly curved (Text-fig. 169).

The subgenus *Heliconius,* which is characterized by the broad duct from the spermathecal diverticulum (Text-fig. 16), the arrangement of the androconia around the hindwing veins Sc + R1 and Rs (Text-fig. 31) and the five-articled female protarsus (Text-fig. 13), is divisible into two classes on the presence or absence of signa on the bursa copulatrix (Text-figs. 26, 28). However, it is suggested that the loss of the signa has occurred at least twice independently, once in the *natteri* group and secondly in the mutual ancestor of the *hecalasius* and *charitonius* groups.

The signate groups of *Heliconius* sensu stricto can be separated into groups on the shape of the



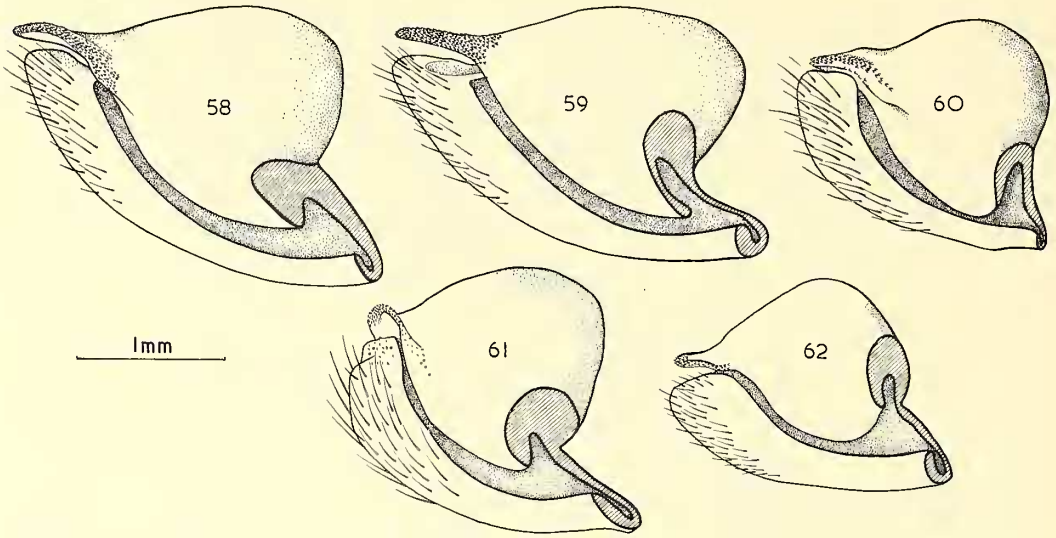
TEXT-FIGS. 52-57. Inner aspect of left genital valves of male *Heliconius*. **52,** *H. godmani;* **53,** *H. aoede;* **54,** *H. metharme;* **55,** *H. doris;* **56,** *H. hecubus;* **57,** *H. xanthocles.*

signa (Text-figs. 148-160), but on its own this character is of limited value for within groups it has no recognizable specific features. The androconial distribution (Text-figs. 81-118) shows more variation within groups in that one or more members usually has an extensive distribution. The male genital valves have to be used with discretion, for though most of the groups have characteristically distinct shapes (Text-figs. 40-74), within the groups only occasionally do they provide valuable specific characters. The red basal spots are widely distributed throughout the subgenus and at least one member of each group exhibits them and in some groups they are a very conspicuous feature (Text-figs. 119-147). No consistent variation was noticed in the female foretarsi within the subgenus *Heliconius* but the relative lengths of the paronychial processes are different in some groups, the most noticeable being the extreme reduction in the *charitonius* group.

The *natteri* group, which contains only *H. natteri,* forms a link between the two subgenera. It is allied to *Heliconius* s.s. in the appearance of the male genital valves (Text-figs. 45, 46-51), yet the androconia though restricted to the hindwings are confined to the veins, as is typical of *Eueides* (Text-fig. 81). As in most of the species which are considered primitive, the female abdominal processes are slender and straight. The absence of signa is considered a loss, as signa are of wide occurrence in the subfamily and other Papilionoidea.

It does not seem possible to indicate which of the groups containing *hierax, godmani, wallacei, doris, hecubus* and *numatus* are the most primitive as they all have members with and without extensive venal androconia; nor does the shape of the signa assist in this connection, as it has already been noticed in *Eueides* that the differences between the signa of two species which are closely related *(pavanus* and *vibilius)* can be as great as that between two groups. However it does seem that the *hecalasius* and *charitonius* groups are more advanced, as they have terminally reduced genital valves, no signa, no androconia on forewing veins other than marginally on 1A, and the hindwing androconia are sparse.

Though *hierax* is differentiated here as a separate group on account of the unique signa (Text-fig. 155) and androconial distribution (Text-fig. 82), the male genital valves are similar in design, though not in development, to those of the *wallacei* group (Text-figs. 40-43), a similarity that is also in evidence in the basal spot complex (Text-figs. 121, 123-125). The female processes are straight and slender (Text-fig. 161), which is considered a primitive feature.



TEXT-FIGS. 58-62. Inner aspect of left genital valves of male *Heliconius*. **58**, *H. hecalasius;* **59**, *H. longarenus;* **60**, *H. erato;* **61**, *H. hermathenae;* **62**, *H. himerus.*

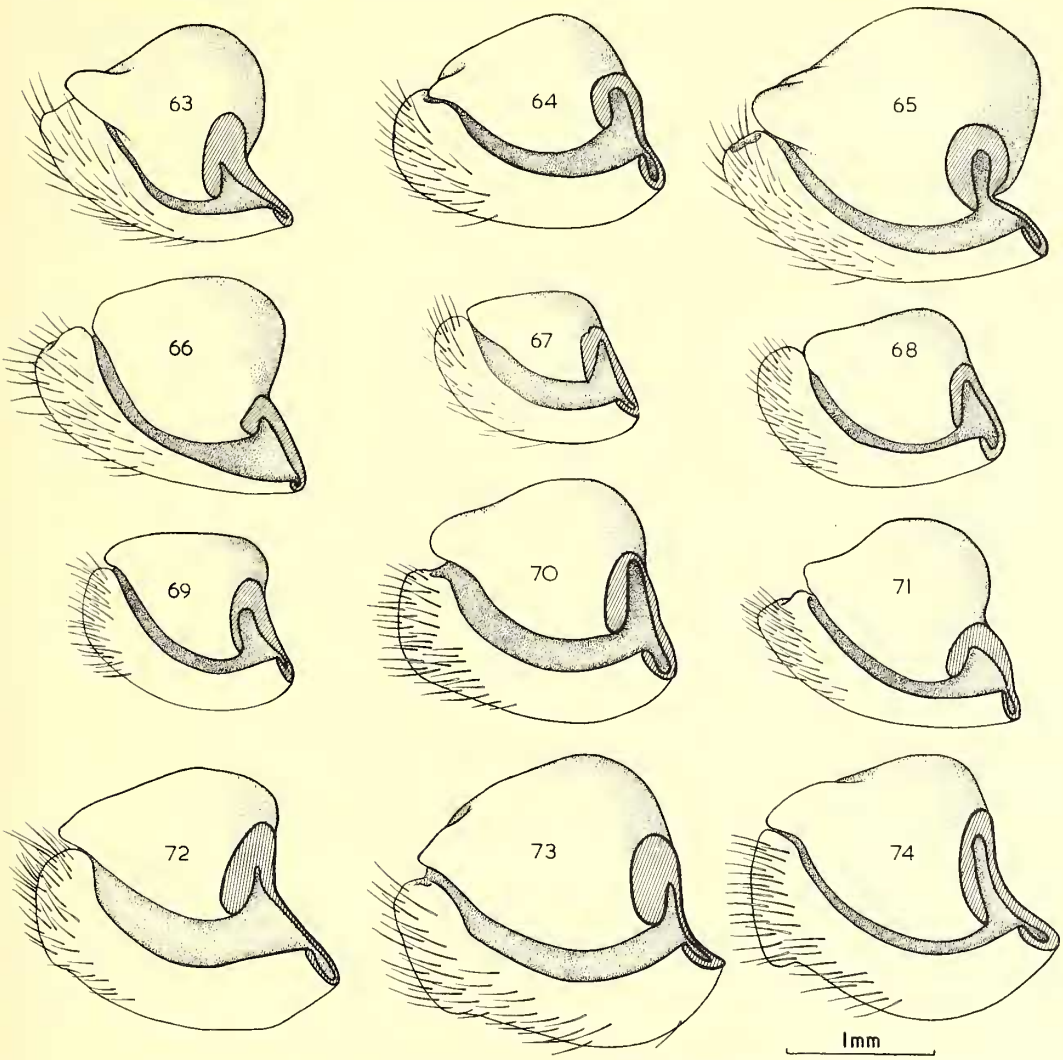
The *wallacei* group have affinities with both *hierax* and the *godmani* group for there is in each a tendency towards an arcuate signa (Text-fig. 157), and there is a similar tendency in *aoede* (Text-fig. 85) and *egerius* (Text-fig. 88) for the androconia to be dispersed over the anterior membrane of the hindwing.

The *godmani* group are homogeneous, the genital valves are very similar (Text-figs. 52-54), there is an unusually tubular spermatheca (Text-fig. 17), and the signum is reduced to a regularly curved slender arc (Text-fig. 156). The main variation is in the localization of the androconia to the veins of the hindwing (Text-figs. 83-85) which in *godmani* is reminiscent of *natteri* (Text-fig. 81).

Heliconius doris is difficult to place, as outside *H. elevatus* and the *charitonius* group it is the only species that has red on the hindwing costal streak, but the shape of the signa (Text-fig. 27) is intermediate between that of the *godmani* and *wallacei* groups and the male genital valves can be allied most clearly with those of the *wallacei* group (Text-fig. 55). Though the gross appearance of the color-pattern is typical of many species of *Heliconius,* non-red ray features are unique (Text-figs. 7, 9).

The two species *H. hecubus* and *xanthocles,* though quite dissimilar in appearance, have almost identical male genital valves (Text-figs. 56, 57) which are distinguishable from those of all other groups, though those of closest affinity seem to belong to the *wallacei* and *godmani* groups. The presence of androconia on the forewing veins in *hecubus* (Text-fig. 99) is considered a primitive character and the differences in the signa (Text-figs. 158, 159) suggests that these two species have been distinct for a relatively long time.

All the groups discussed so far have straight, slender female abdominal processes and have denticles along the greater part of the dorsal component of the male genital valve, both of which are characters which are considered to be primitive in the genus. The only remaining signate group for discussion is the *numatus* group, which is characterized by the restriction of denticles on the male genital valves to the apex of the dorsal component and the internal position of the ventral component (Text-figs. 46-51). The denticles at the base of the dorsal component in *melpomene* (Text-fig. 46) and *cydno* (Text-fig. 47) may be a vestige of the ancestral distribution which has persisted in the more primitive species. The valves of the pairs of species *elevatus* and *ethillus* (Text-fig. 51) and *cydno* and *pachinus* (Text-fig. 47) cannot be distinguished and even the valves of *numatus* (Text-fig. 48) and *aristionus* (Text-fig. 51) can only be distinguished with a series of each. Within the group the radius of deflection of the signa varies, but in all species the posterior arm is relatively long (Text-figs. 26, 160). *H. numatus* has androconia on many of the fore and hindwing vein (Text-figs. 101, 92), *aristionus* and *elevatus* have them on several hindwing veins and forewing veins 1A, but *mel-*

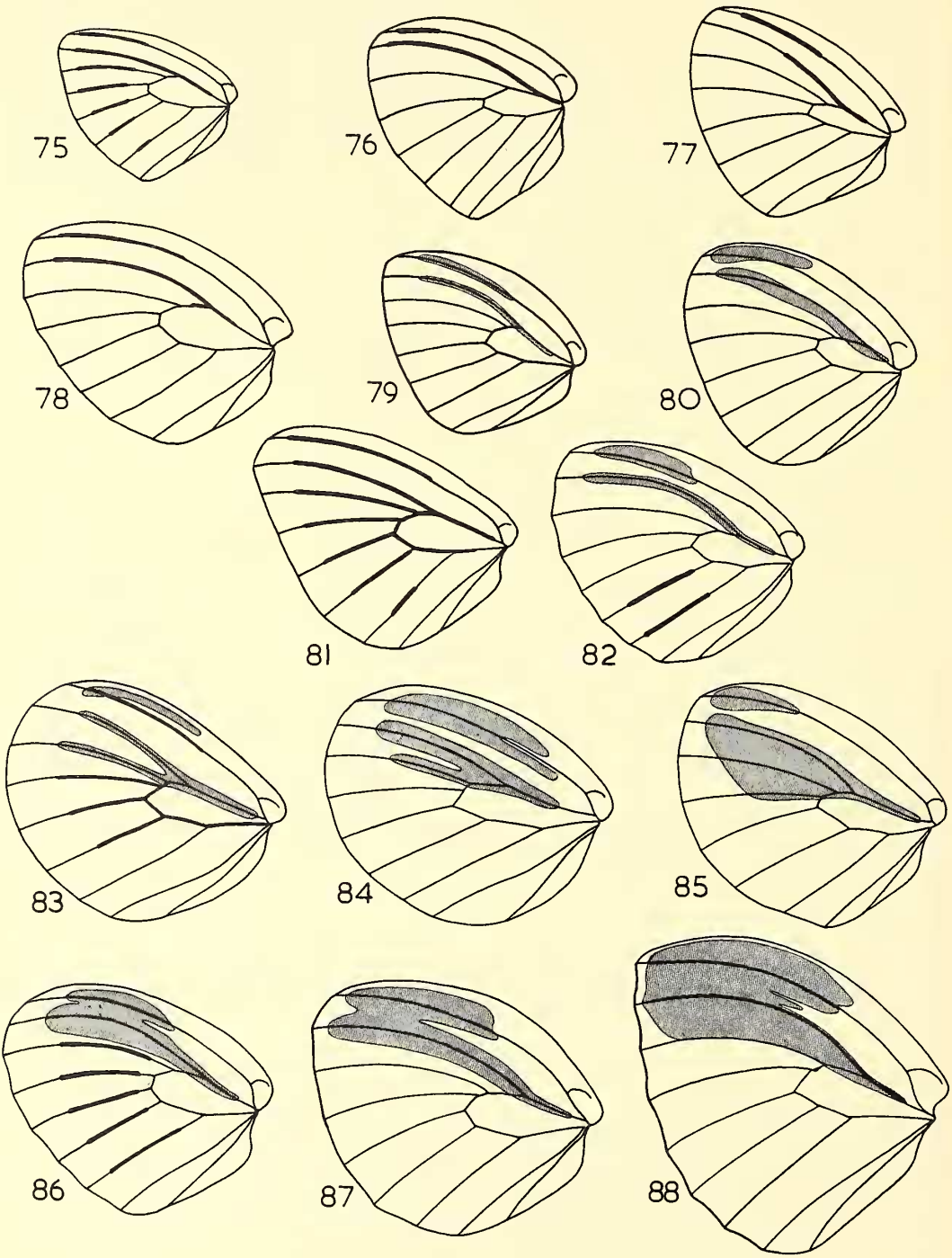


TEXT-FIGS. 63-74. Inner aspects of left genital valves of male *Heliconius*. **63,** *H. telesiphe;* **64,** *H. charitonius;* **65,** *H. hortense;* **66,** *H. clysonymus;* **67,** *H. ricini;* **68,** *H. demeter;* **69,** *H. sarae;* **70,** *H. leucadius;* **71,** *H. hygianus;* **72,** *H. sapho;* **73,** *H. antiochus;* **74,** *H. hewitsoni.*

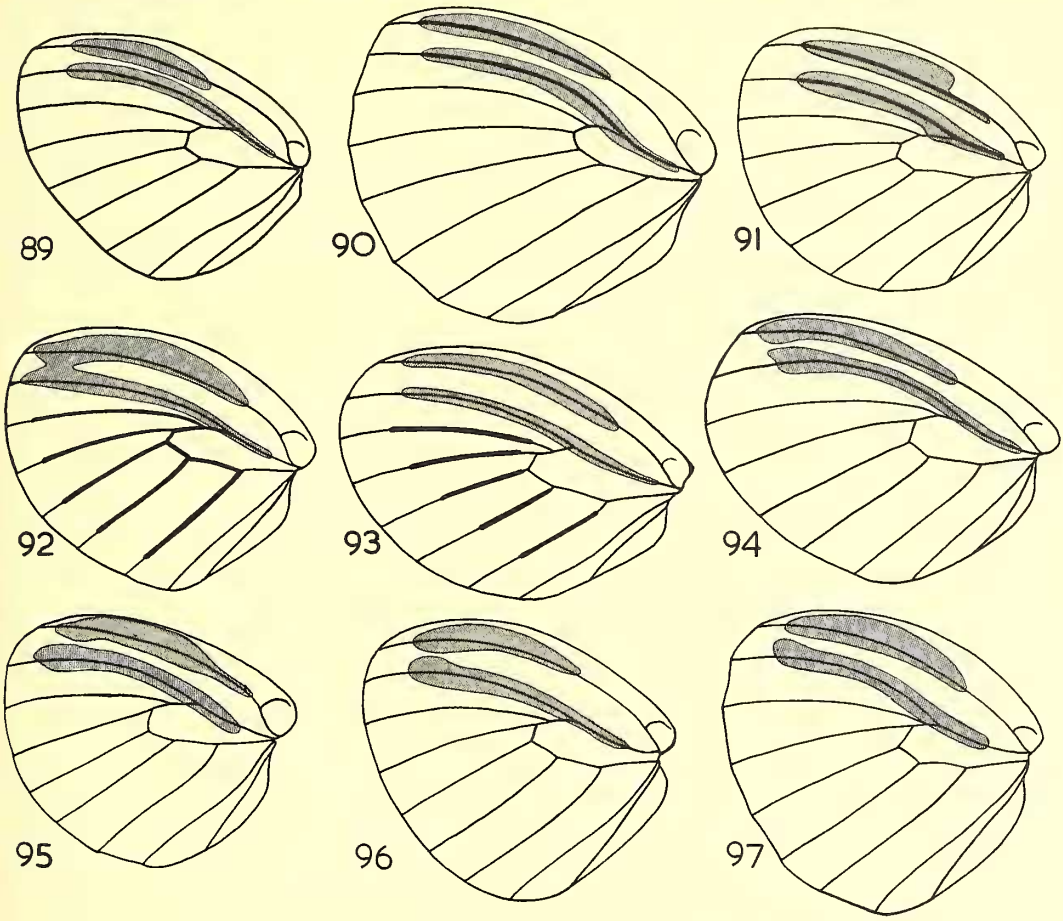
pomene, ethillus, atthis, hecale, cydno and *pachinus* have them only on the veins Sc + R1 and Rs (Text-figs. 94-97) of the hindwing and forewing vein 1A. The development of the red basal spots varies from complete absence without trace in *cydno, hecale* and *numatus,* through the retention of a single spot in *atthis, aristionus, ethillus* and *elevatus* (Text-figs. 129, 130), to reasonably complete development in *melpomene* (Text-fig. 131). The condition in *pachinus* is unlike that of any other species and is discussed in the next section (Text-fig. 128). The similarity between the androconial distribution of *wallacei* and *numatus* is attributed to the persistence of a primitive condition and as in the other groups there is a trend towards an even but dense distribution of androconia around the hindwing veins Sc + R1 and Rs.

The non-signate groups, other than *natteri,* are the *hecalasius* and *charitonius* groups which are assumed to have evolved from a common non-signate ancestor.

The *hecalasius* group contains *hecalasius, himerus, telesiphe* and *hermathenae* which by vir-



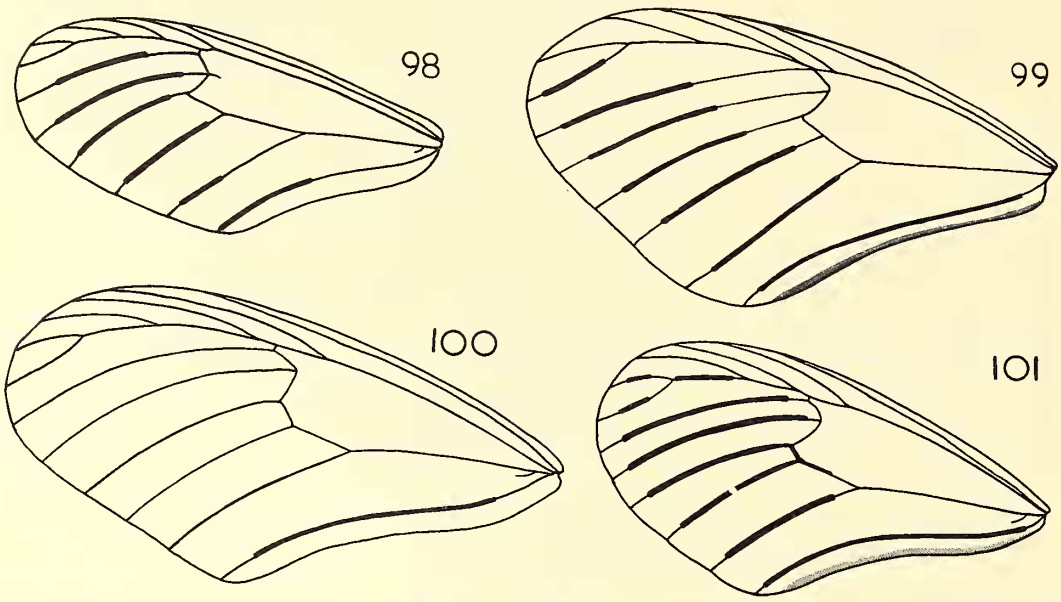
TEXT-FIGS. 75-88. Dorsal view of left hindwings of male *Heliconius* to illustrate the variation in the distribution of androconia. **75,** *H. alipherus;* **76,** *H. edias* or *H. vibilius;* **77,** *H. eanes* or *H. lineatus;* **78,** *H. isabellae;* **79,** *H. lybius;* **80,** *H. tales;* **81,** *H. natteri;* **82,** *H. hierax;* **83,** *H. godmani;* **84,** *H. metharme;* **85,** *H. aoede;* **86,** *H. wallacei;* **87,** *H. burneyi;* **88,** *H. egerius.* About twice natural size.



TEXT-FIGS. 89-97. Dorsal view of left hindwings of male *Heliconius* to illustrate the variation in distribution of androconia. **89,** *H. doris,* **90,** *H. hecubus;* **91,** *H. xanthocles;* **92,** *H. numatus;* **93,** *H. aristionus* or *H. elevatus;* **94,** *H. ethillus;* **95,** *H. atthis;* **96,** *H. melpomene;* **97,** *H. cydno.* About twice natural size.

tue of their unusually extensive androconial distribution are considered more primitive than *erato, longarenus, clysonymus* and *hortense* (Text-figs. 102-108, 110). The genital valves of male *hecalasius* (Text-fig. 58), *longarenus* (Text-fig. 59), *hermathenae* (Text-fig. 61), *erato* (Text-fig. 60) and *himerus* (Text-fig. 62) are basically similar and have terminal denticles which are absent from the valves of *telesiphe* (Text-fig. 63), *clysonymus* (Text-fig. 66) and *hortense* (Text-fig. 65). All the members of the group have basal spots except *hecalasius* and *longarenus* (Text-figs. 132-136, 140). The reduction of the androconia on the media veins of the hindwings of specimens of *hecalasius* from southern localities opens up the possibility that *longarenus,* which has none, is conspecific; otherwise they are morphologically similar and in color-pattern not basically different. The unexamined *gynaesius* may be of assistance in this problem. Though the red forewing band of *hermathenae* is considered of independent origin from that occurring in *erato,* there is a similarity in the arrangement of the supernumerary basal spots (Text-figs. 136, 140) which suggests a close relationship, for the arrangement of the proximal basal spots on the other species in the group is relatively uniform (Text-figs. 132-136, 140).

The *charitonius* group is morphologically exceedingly uniform. The female processes are short and squat (Text-fig. 172), the male genital valves are almost indistinguishable (Text-figs. 64, 67-74) except for a tendency in *antiochus, sapho* and *hewitsoni* for the lower limb to be ventro-distally thickened (Text-figs. 70, 72-74). The androconia are confined exclusively to the hindwing veins Sc + R1 and Rs and narrowly to the membrane around them (Text-figs. 111-115), or in some cases *(antiochus, sapho* and *hewitsoni)* not even on the membrane around Rs (Text-figs.



TEXT-FIGS. 98-101. Dorsal view of left forewings of male *Heliconius* to show variation in androconial distribution. **98**, *H. edias;* **99**, *H. hecubus;* **100**, *H. ethillus;* **101**, *H. numatus.* About twice natural size.

116-118). A subdivision within the group can be identified by the red hindwing costal streak, a character known elsewhere in the genus only in *H. doris* and *H. elevatus;* these species comprise *sarae, leucadius, hygianus, sapho, antiochus* and *hewitsoni* (Text-figs. 141-147). The remaining species are *charitonius, ricini* and *demeter* which are normal in that the hindwing costal streak is yellow. *H. demeter* is unusual in that the forewing costal spot is yellow too, a condition known elsewhere in the subgenus only in *H. egerius. H. leucadius* seems to occupy a position intermediate between the *sapho* sub-group and *sarae* and *hygianus* (see Text-fig. 173).

V. Evolutionary Discussion

So far in this systematic study, a deliberate attempt has been made to avoid using the more obvious color-patterns of the wings, as it is likely that there are similarities due to convergence. However, when the color-patterns are considered in relation to geographic distribution, they provide useful data.

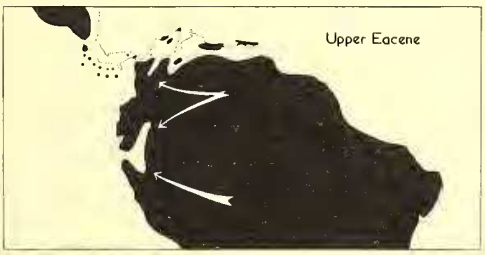
The over-all range of the genus *Heliconius* can be divided into five zones: Central America and northern Colombia; western Ecuador and western Colombia; eastern Ecuador, Peru and Bolivia above 850 meters; coastal Brazil; and the Amazon basin. Before launching a hypothesis to explain the present diversity of the genus, an account must be given of the geographic history of the relevant portions of the American continents.

Palaeogeographers are not in complete agreement over the details of the continuity of the land masses in the early Tertiary, but here the views of Weeks (1947) and Lloyd (1963) have been followed and the four maps (27-30) drawn from their data. The geological evidence suggests that the maximum distance between the continents during the Upper Eocene was 650 miles (Map 28), but in the absence of fossils it is difficult to estimate how much of a barrier this was to the dispersal of mobile Papilionoidea. Though the distance was greater than this in the Palaeocene and Oligocene (Maps 27, 29), there were always some islands which could have acted as stepping stones.

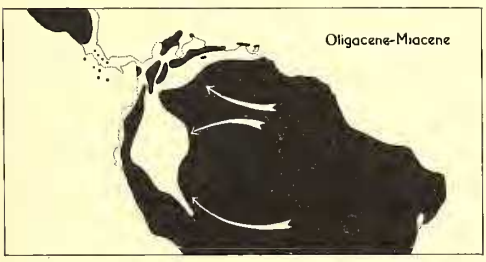
The neotropical Heliconiinae seem the only major subdivision of the Nymphalidae which are confined to one zoogeographical region. Some Australasian and Oriental genera have been examined, but no heliconiine characters have been found. The restricted distribution could be due either to all the non-neotropical representatives having become extinct, which in view of the success enjoyed in South America seems unlikely, or the group could have evolved at a time when it was too late to disperse laterally into the other continents because of the low northern temperatures.

The Lamaride revolution, which produced the Rocky and Andean mountain chains, began in

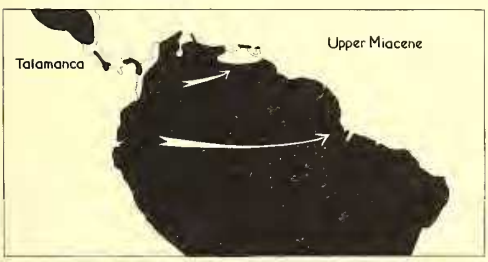
MAP 27



MAP 28



MAP 29



MAP 30

the Cretaceous and by the Eocene had elevated the row of large islands seen in Map 27. This uplift changed the course of the drainage in South America from the east-west direction of the Palaeocene epoch (Map 27) to the northerly outlet of the Oligocene (Map 29). The Guianian and Brazilian mountains are not figured on the maps, but they are known to have been a dominant feature of the geography of the continent since the Pre-cambrian and have undoubtedly impeded the dispersal of *Heliconius* around coastal Brazil.

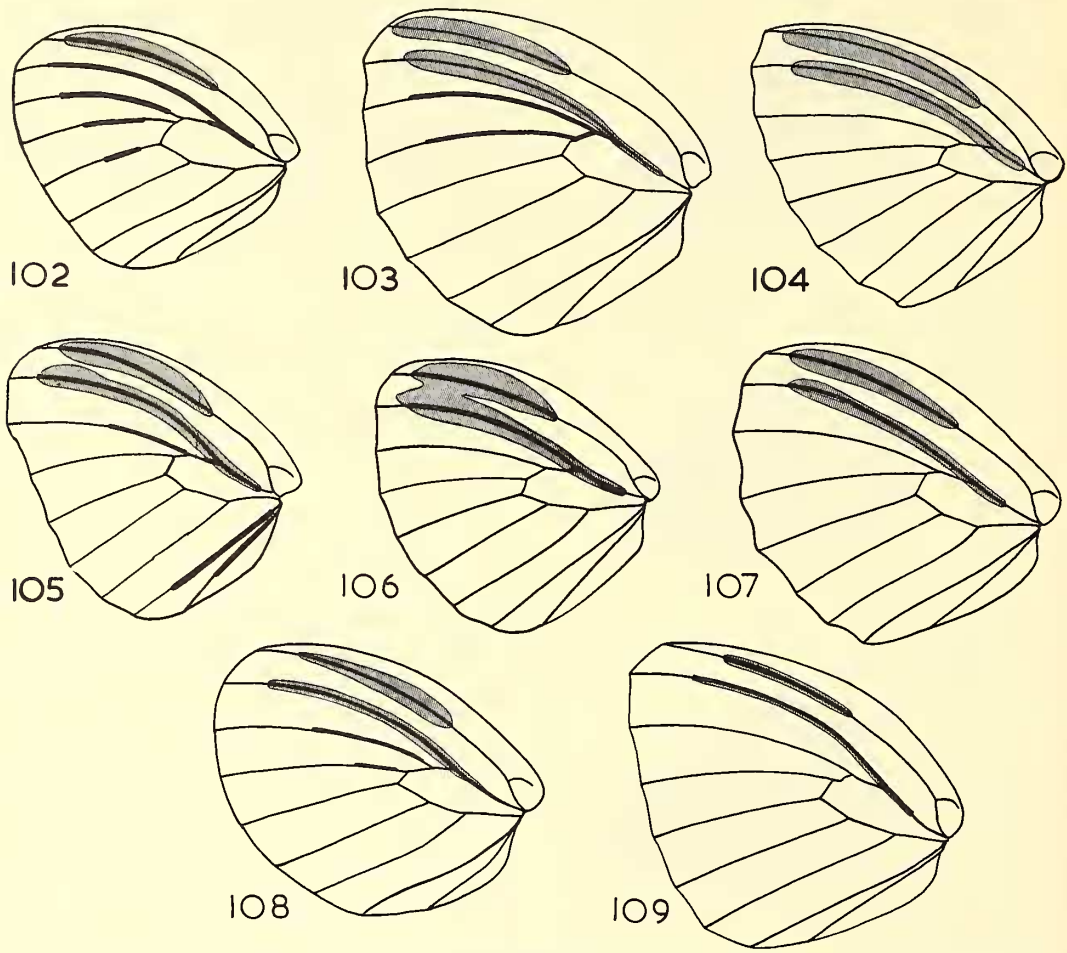
The second main wave of Andean orogeny occurred at the end of the Miocene and raised the western continent to such an extent that the drainage changed to that known today, with the consequent silting up of the inland sea of the early Miocene (Maps 29, 30). This period was probably the critical phase in the evolution of *Heliconius,* for there would have been the opportunity for the colonization of a new area of land, and not just competitive incursion into a territory already occupied by a well-established flora and fauna. It may well have been a critical phase in the evolution of *Passiflora* too, but there is insufficient data to consider the interaction of the larval foodplants at this stage of our knowledge.

In the following hypothesis it is assumed that the two subgenera of *Heliconius* were already distinct at the time of incursion into South America. Within the more primitive subgenus *Eueides* the stable species *alipherus, lybius, lineatus* and to a lesser extent *vibilius* still exhibit the ancestral color-pattern also retained by *Colaenis iulia.* Of the species listed, only the Central American *lineatus* is not widely distributed and it may be a relic of the North American fauna which survived on the southern peninsula while the main evolution of the genus was taking place in South America.

The hypothesis assumes that the invasion of South America took place during the Eocene and Oligocene so that by the beginning of the Miocene the main species groups had become differentiated, and the whole of the continental area that was ecologically suitable had been colonized. The geography of South America at this time, about 25 million years ago, is shown on Map 29. The western peninsula was isolated by water on all sides except the south where the mountains may or may not have acted as a barrier. As the orogenic movements increased, the fauna of the western slopes would still have been isolated even after the establishment of land continuity to the east, but by mountains instead of water. It is on these western slopes that we now find the peculiar species *atthis, godmani, longarenus* and *hygianus,* each of which belongs to a distinct species group. It is suggested that these species are endemic.

The small number of species that have colonized eastern Brazil is probably due to the narrow entrance to the coastal plane that lies between the Brazilian highlands and the sea. Only *H. natteri* and *pavanus* are considered truly native.

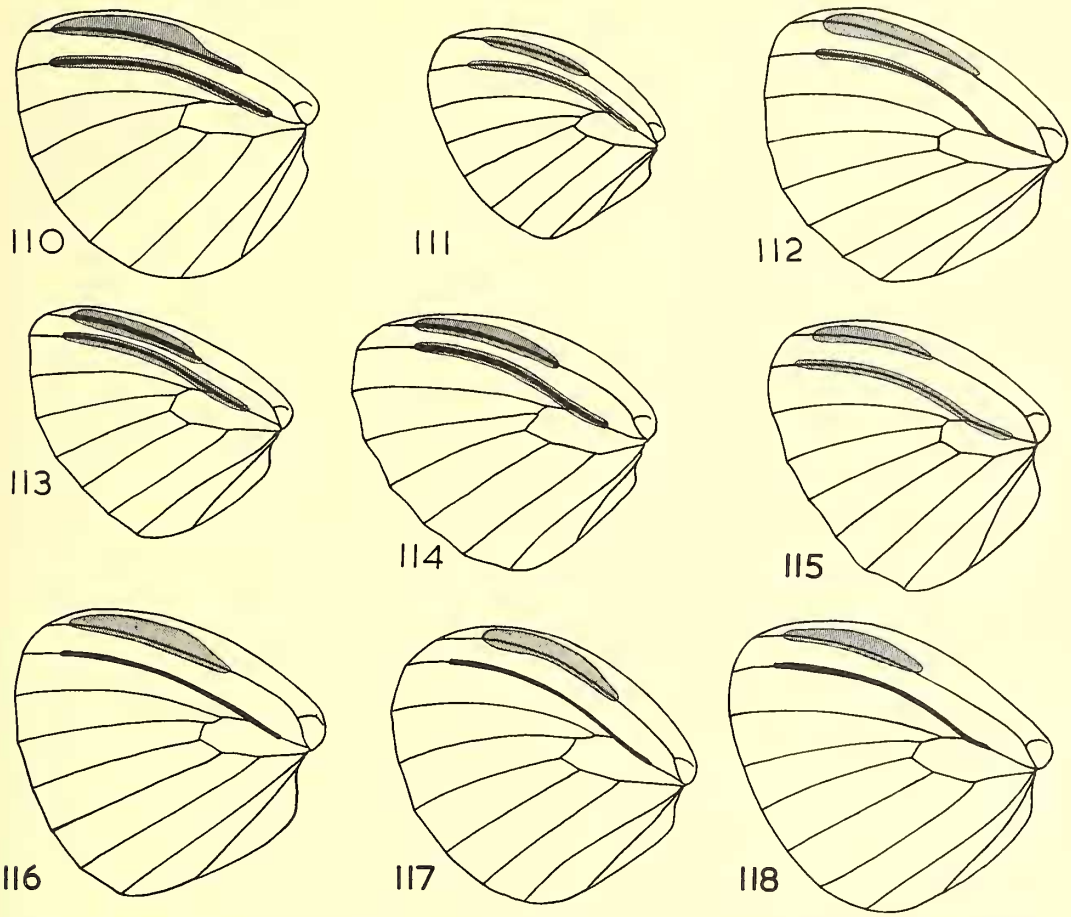
In the northwestern part of South America



TEXT-FIGS. 102-109. Dorsal view of left hindwings of male *Heliconius* to illustrate variation in the distribution of androconia. **102,** *H. himerus;* **103,** *H. hecalasius;* **104,** *H. longarenus;* **105,** *H. telesiphe;* **106,** *H. clysonymus;* **107,** *H. hortense;* **108,** *H. hermathenae;* **109,** *H. charitonius.* About twice natural size.

during the early Miocene there were a few large islands which had been united in the Eocene. It is suggested that it was on these islands that the endemic fauna of northern Colombia originated, some species of which have since extended their range. These endemic species are *edias, hecubus, hecalasius, cydno, sapho, clysonymus* and *charitonius.* It is probably also from this center that *telesiphe* spread southwards down the eastern side of the Andes. The existence of *cydno* and *sapho* stock material in this area in the Upper Miocene could account for the present distribution of *pachinus* and *hewitsoni,* for it was about this time that the Talamanca island first appeared (Map 30). If the precursors of *cydno* and *sapho* had managed to colonize Talamanca in the Upper Miocene, there would have been time for reproductive isolation to have occurred before the parent species advanced up the elevated isthmus of Central America in the Pliocene. The present distribution of both *pachinus* and *hewitsoni* is at the southern extremity of the Talamanca ridge and the islands off-shore. If this is correct, *H. lybius lybioides* may well have had a similar origin, for it too is peculiar to the Chiriqui volcano and the immediate neighborhood. Further work may show that it is specifically distinct from the closely related *H. lybius olympius* which inhabits the surrounding areas of Central America.

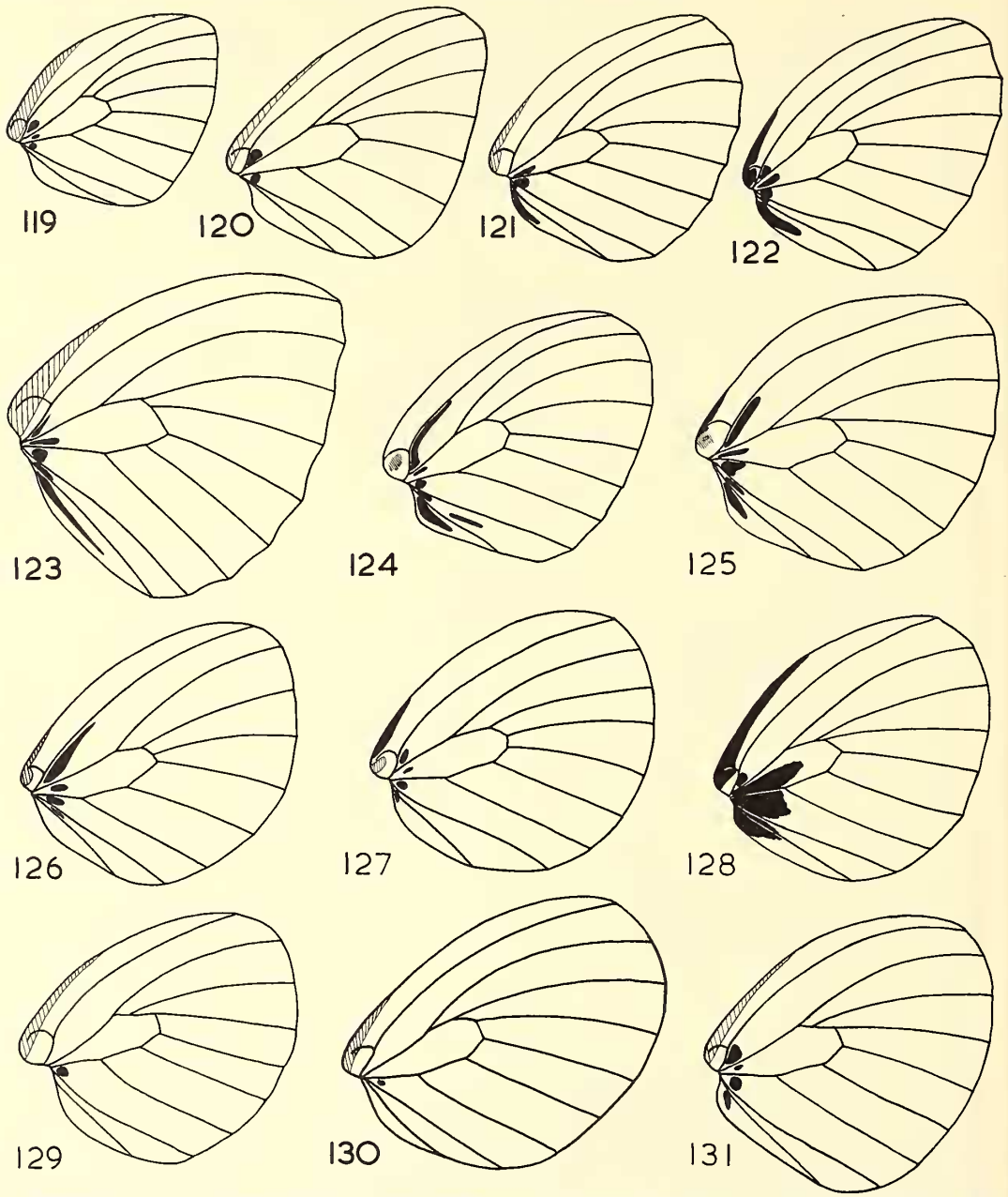
The two species *hewitsoni* and *sapho* are morphologically almost identical, as are *pachinus* and *cydno.* However, *hewitsoni* and *pachinus* are very similar in color-pattern, and so are *sapho*



TEXT-FIGS. 110-118. Dorsal view of left hindwings of male *Heliconius* to illustrate variation in the distribution of androconia. **110,** *H. erato;* **111,** *H. ricini;* **112,** *H. demeter;* **113,** *H. sarae;* **114,** *H. leucadius;* **115,** *H. hygianus;* **116,** *H. sapho;* **117,** *H. antiochus;* **118,** *H. hewitsoni.* About twice natural size.

and *cydno*. The relationships among these four species are therefore of some interest. *H. hewitsoni* has very large hindwing red basal spots and belongs to a species-group in which they are always very conspicuous. *H. pachinus* also has very large basal spots, but these are of a unique character, and its closest relatives have either very small spots or no spots at all *(H. cydno)*. The spots of *pachinus* do not conform to the pattern which is common to all other species of *Heliconius*, and the edges of the spots are of an appearance unknown elsewhere. It is suggested that the red basal spots of *pachinus* are not homologous with those of *hewitsoni* but have been evolved from a non-spot ancestor such as *cydno*. The remarkable similarity between these two sympatric species suggests a mimetic relationship which may be similar to that between *cydno* and *sapho*. If the relationship is Müllerian, then it would have been advantageous for *hewitsoni* and *pachinus* to have rapidly become as similar as possible, and one would have expected the red basal spots of *hewitsoni* to have become reduced to the smallest dimensions that were commensurate with the efficient performance of their function. Similarly, if *pachinus* had had red basal spots or had acquired them later, they should have increased in size until they matched those of *hewitsoni*. But we find that the basal spots of *hewitsoni* are much larger than is usual, as if it is advantageous for it to maintain its identity. The situation suggests that relationship is Batesian rather than Müllerian.

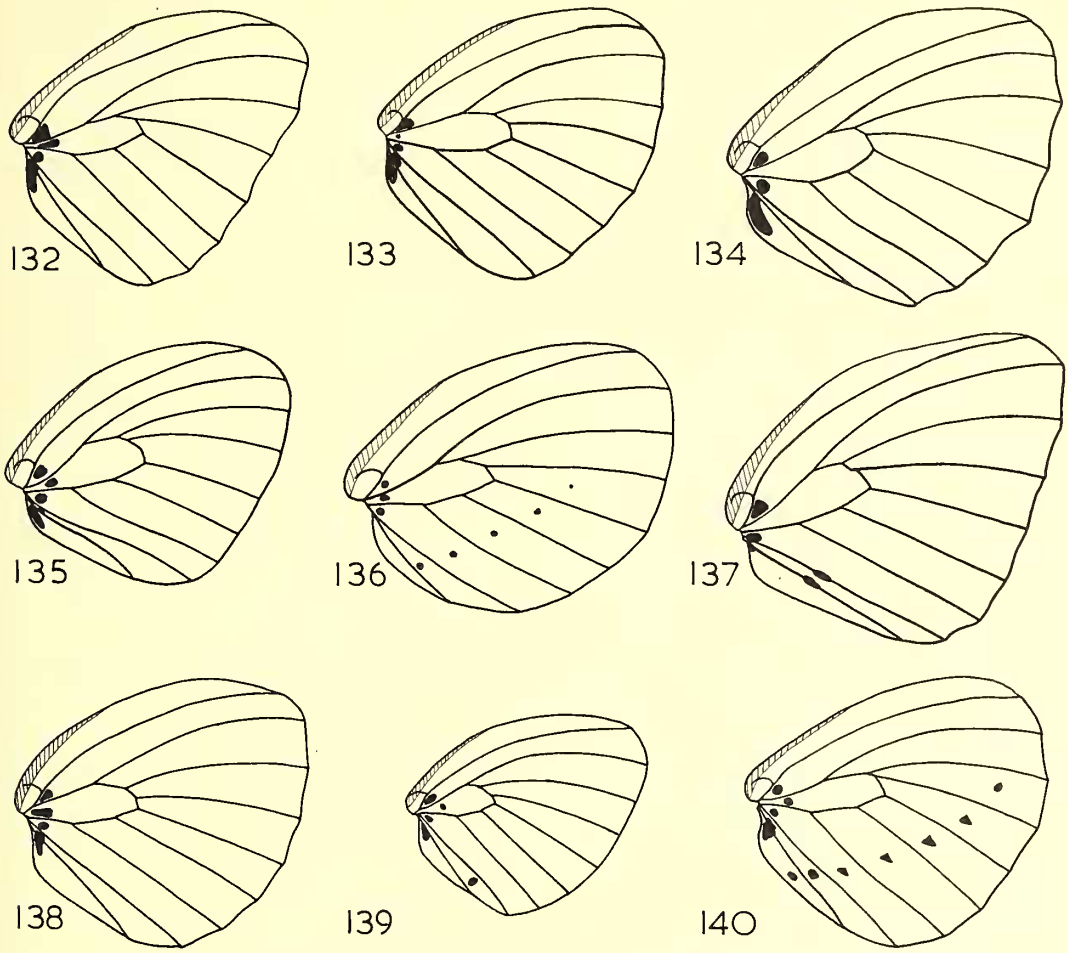
The closeness of the match of the color-pattern in *cydno* and *sapho* leaves no doubt that the relationship is mimetic, and *H. cydno* may lack basal spots because, unlike *pachinus*, it has not yet re-evolved them. If these arguments are cor-



TEXT-FIGS. 119-131. Ventral view of left hindwings of *Heliconius* species to illustrate variation in the basal spot complex. **119,** *H. lybius lybius;* **120,** *H. natteri;* **121,** *H. hierax;* **122,** *H. doris;* **123,** *H. egerius;* **124,** *H. wallacei;* **125,** *H. burneyi;* **126,** *H. aoede;* **127,** *H. xanthocles;* **128,** *H. pachinus;* **129,** *H. atthis;* **130,** *H. ethillus* or *H. aristionus;* **131,** *H. melpomene.* About twice natural size.

rect, palatability trials with suitable predators should reveal that *hewitsoni* and *sapho* are both more distasteful than *pachinus* and *cydno*. If, however, the red basal spots are important in courtship as a recognition mechanism, then the persistence of this character may be necessary in *sapho* for reproductive isolation. This could be investigated experimentally.

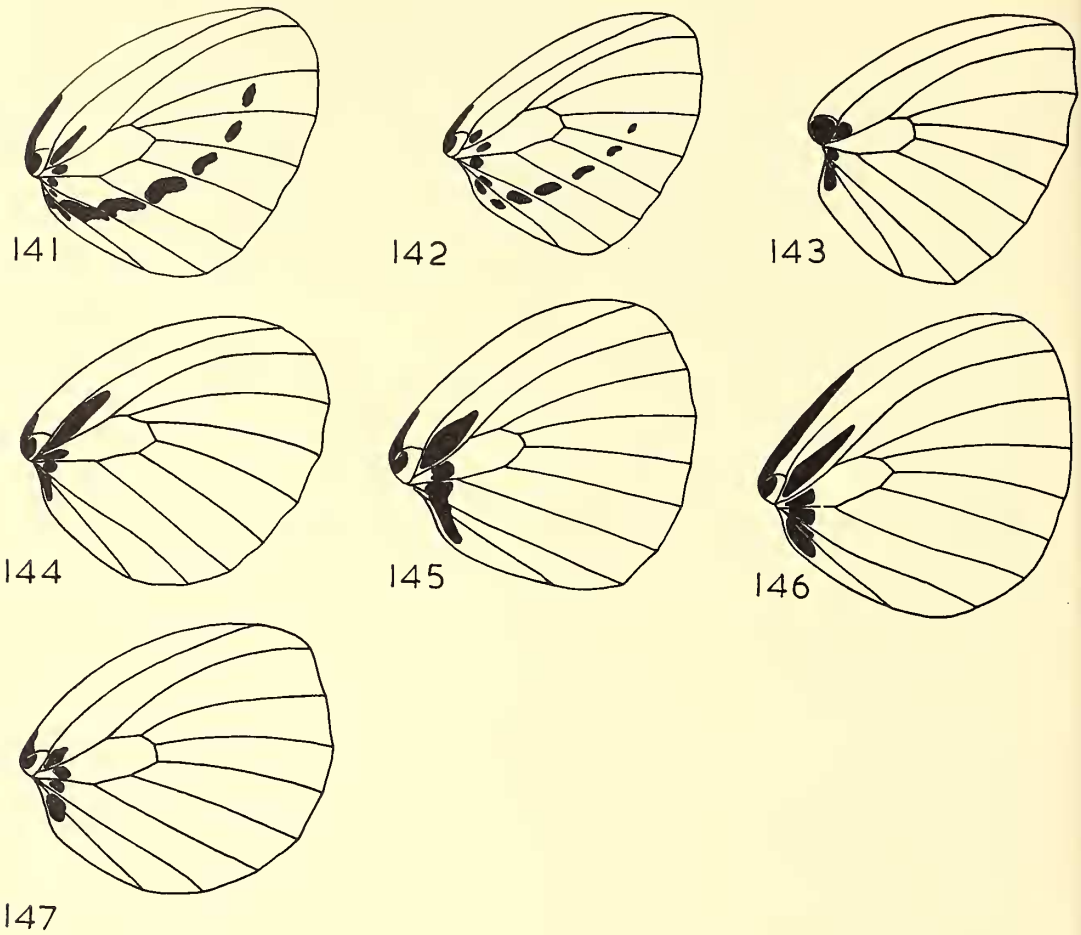
While these northwestern species were differentiating in what are now the Colombian Andes, the main evolution of the genus was taking place in eastern Ecuador and northeastern Peru. With



TEXT-FIGS. 132-140. Ventral view of left hindwing of *Heliconius* species to illustrate variation in red basal spot complex. **132,** *H. telesiphe;* **133,** *H. clysonymus,* **134,** *H. hortense;* **135,** *H. himerus;* **136,** *H. hermathenae;* **137,** *H. charitonius;* **138,** *H, demeter;* **139,** *H. ricini;* **140,** *H. erato.* About twice natural size.

the continued uplift of the Andes towards the end of the Miocene, the inland sea (Map 29) was drained, and *Heliconius* seems to have exploited the opportunity for recolonization. The present Amazonian representatives of the genus, with the exception of *hermathenae,* exhibit only two types of color-pattern. These are a more or less iridescent blue ground color with one or two yellow forewing bands *(wallacei, metharme, sarae, antiochus, leucadius, sapho congener* and *doris doris),* and a complex pattern which displays a black wing tip, a yellow forewing band of variable width and an orange or red wing base. This black-yellow-red (B-Y-R) pattern may be achieved by the expression of dennis and ray characters (Text-figs. 5-8, 10) as in the species *eanes, tales, aoede, burneyi, egerius, xanthocles, elevatus, melpomene, erato, demeter* and *doris delilae,* or by variation in expression of spots and bars as in *isabellae, numatus, aristionus* and *ethillus.*

The dennis-ray species of wide distribution acquire other patterns beyond the limits of the Amazon basin and exhibit acute polychromatism in the transitional zones of central Colombia, the Guianas, central Bolivia and at about the 850 meter level in the Ecuadorian Andes, and at comparable ecological levels to the north and south. The species which behave most spectacularly in this respect are *melpomene* and *erato,* for in both the forewing band changes from yellow to red, dennis and ray are lost, and a yellow hindwing bar and increased iridescence acquired. This has been described and discussed in detail



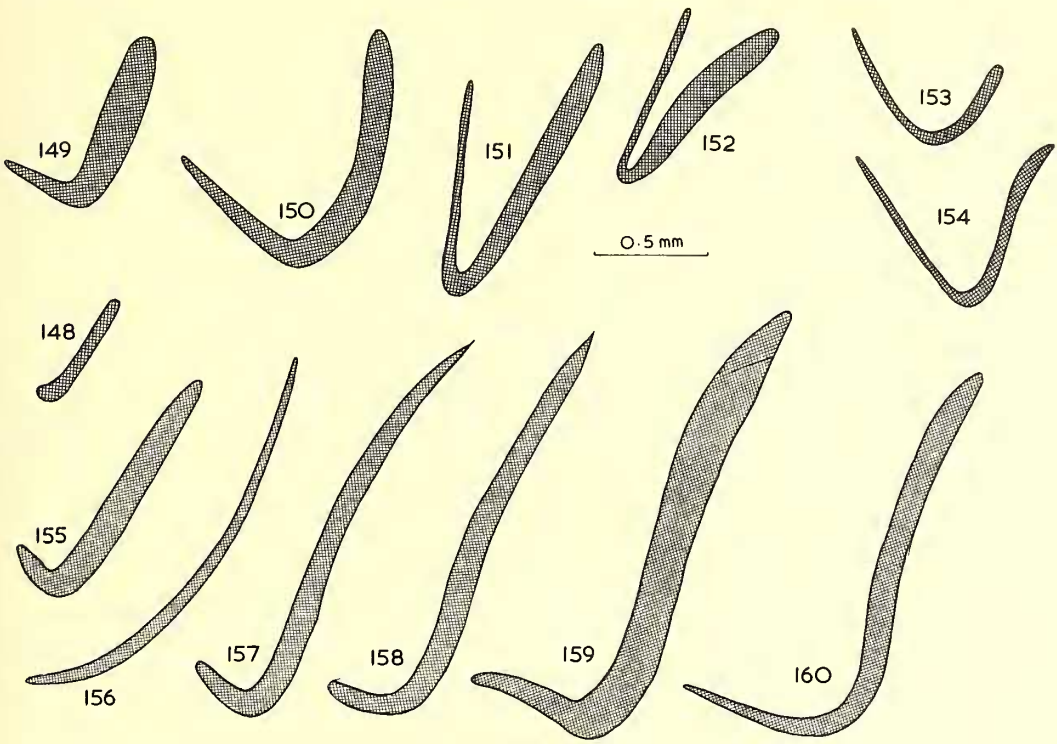
TEXT-FIGS. 141-147. Red basal spots in *Heliconius*. **141,** *H. leucadius;* **142,** *H. sarae;* **143,** *H. hygianus;* **144,** *H. antiochus;* **145,** *H. sapho sapho;* **146,** *H. hewitsoni;* **147,** *H. sapho congener*. About twice natural size.

in Emsley (1964). The Amazonian species which effect the B-Y-R pattern with spots and bars change most obviously in the eastern Andes, where the patterns of *numatus, ethillus, aristionus, isabellae* and *vibilius* become more extensively orange and black at the expense of the yellow. There is no experimental and little observational evidence to suggest the cause of the apparently strong selection for a B-Y-R pattern in the Amazon basin, but the most likely explanation, for which some evidence was offered in Emsley (1964), is that it is due to a mimetic situation in which the Danainae act as models. The systematics and evolution of the Danainae are pertinent and should be investigated. To what extent Müllerian relationships within *Heliconius* are operative is unknown.

The hypothesis that the species-groups of *Heliconius* had differentiated by the early Miocene is supported by the fact that almost all the groups have at least one member in this Amazonian complex.

A completely unexplained phenomenon is the uniformity of the variation in the shape of the yellow forewing band in all the dennis-rayed species in the Amazon basin. The specimens from the Lower Amazon have a broad spotted forewing band centered over the apex of the discal cell, but specimens from westerly localities have the band narrow and rectangularly compact and distal to the discal cell. There is also a cline in the intensity and development of ray from the Guianas, where it is least, to the south and west where it is most intense.

There is considerable variation in the dennis, ray and forewing band characters of *melpomene*

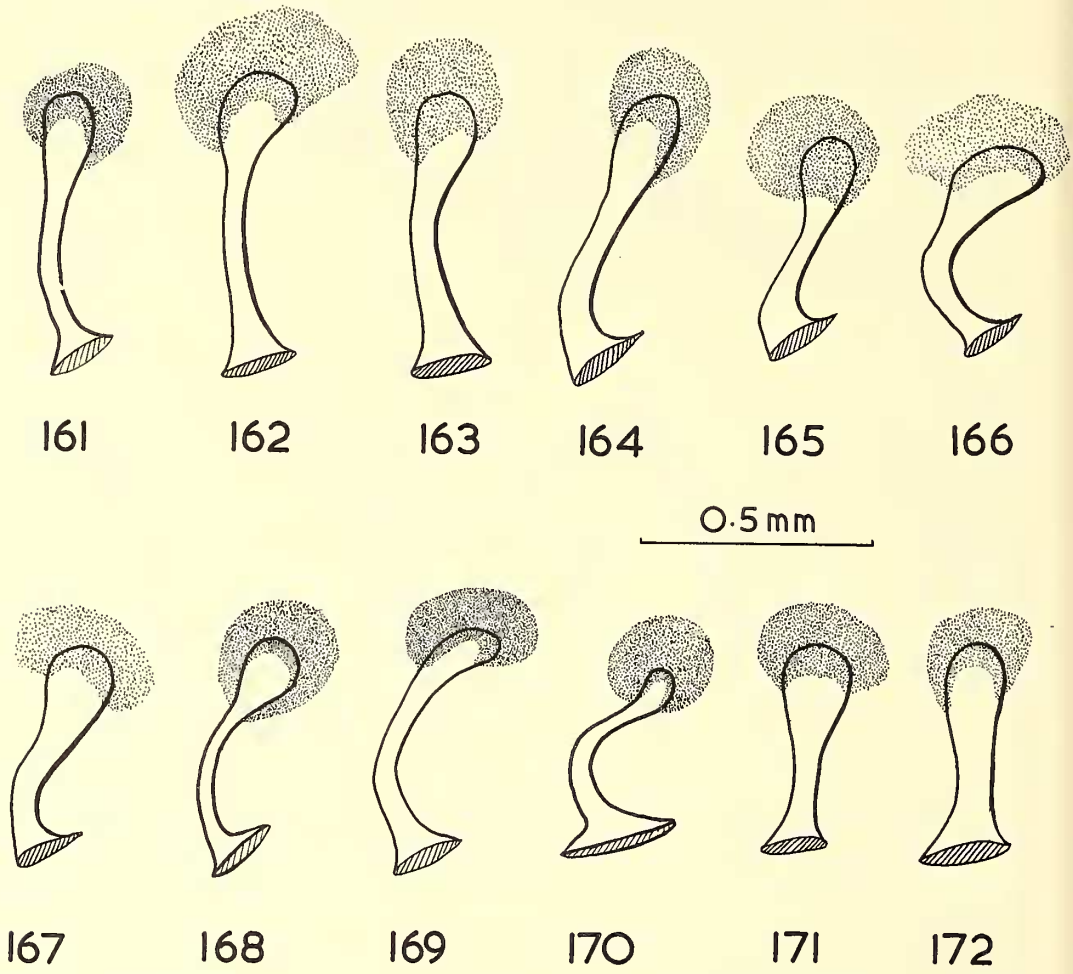


TEXT-FIGS. 148-160. Variation in the shape of the signa in *Heliconius*, as viewed from the right. **148,** *H. pavanus;* **149,** *H. edias;* **150,** *H. lineatus,* or *isabellae,* or *eanes,* or *vibilius;* **151,** *H. lybius* left side; **152,** *H. lybius* right side; **153,** *H. tales* left side; **154,** *H. tales* right side; **155,** *H. hierax;* **156,** *H. aoede,* or *godmani,* or *metharme;* **157,** *H. wallacei* or *burneyi;* **158,** *H. xanthocles;* **159,** *H. hecuba;* **160,** *H. atthis.*

in the vicinity of Obidos, Brazil. West of this area all these butterflies have a yellow forewing band, dennis and ray, but progressing towards the northeast more and more specimens have red on the forewing band and lack dennis and ray. Around Obidos it had seemed that the red-banded non-dennis non-ray form was rare, but a series of reliably labelled specimens in the American Museum of Natural History, all taken from one locality very near Obidos on one occasion, exhibit the red-banded non-dennis non-ray pattern that is characteristic of Trinidadian *melpomene*. Therefore it would seem that selection among the various B-Y-R color-patterns differs not only geographically but perhaps temporally also. A detailed examination of label data might indicate whether these fluctuations are seasonal, annual or irregular.

The only red-banded species other than *erato* and *melpomene* is *H. hermathenae,* which has also been taken from the Obidos area. It is relatively rare and may be maintained at a low population level by periodic "boosts" which select for the red-banded non-dennis non-ray color-pattern in *melpomene* (and *erato?*). The *charitonius*-type yellow markings of *hermathenae* are probably a relatively primitive character, the red of the forewing band having been acquired independently of that of *erato* and *melpomene*.

As the sympatric forms of *numatus, aristionus* and *ethillus* vary together throughout their range, the close similarity in their general appearance suggests a mimetic relationship. In Honduras, where *ethillus* occurs in the absence of *numatus* and *aristionus, ethillus fornarinus* is quite unlike any other form of any other species in the complex. The ventral pattern is like that of *H. cydno,* and the over-all appearance is very similar to that of *H. hecale,* which is an uncommon species restricted to a few localities in the Guianas. Both *cydno* and *hecale* are members of the same species group as *ethillus*. In view of the close systematic relationship between *ethillus* and *hecale,* it is possible that *hecale* represents a relic of the stock from which *ethillus* evolved which has retained the ancestral color-pattern. This is supported by the *hecale*-like appearance of *ethillus* in Honduras, where *numatus* does not occur.

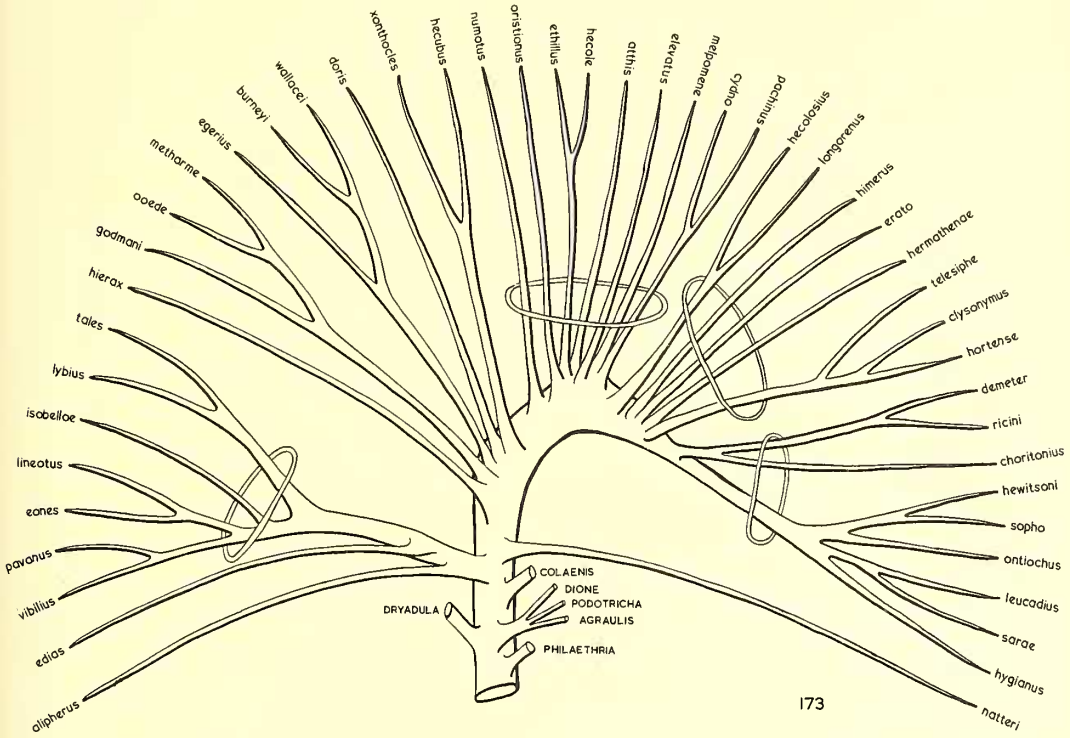


TEXT-FIGS. 161-172. Variation in the shape of the female abdominal processes in *Heliconius*. **161,** *H. alipherus* or *lineatus* or *vibilus* or *eanes* or *isabellae* or *hierax* or *natteri;* **162,** *H. wallacei* or *burneyi* or *egerius;* **163,** *H. xanthocles* or *hecubus* or *doris;* **164,** *H. melpomene* or *cydno* or *pachinus* or *numatus* or *etlulillus* or *aristionus* or *hecale;* **165,** *H. metharme* or *godmani* or *aoede* or *erato;* **166,** *H. hecalasius* or *longarenus;* **167,** *H. hortense* or *clysonymus;* **168,** *H. hermathenae;* **169,** *H. tales* or *lybius;* **170,** *H. edias;* **171,** *H. telesiphe;* **172,** *H. sapho* or *hewitsoni* or *sarae* or *antiochus* or *leucadius* or *hygianus* or *ricini* or *demeter* or *charitonius.*

This is further supported by the occurrence of similar elements of the color-pattern in *cydno*.

Since the species *clysonymus, hortense, himerus, hierax, hygianus* and *ricini* are all allopatric, there are probably no mimetic relationships among them. The red bar on the hindwing may be a persistent primitive character if the ability to produce red pigment were a prerequisite to the colonization of the Amazon basin by the B-Y-R patterned species. The relationship between *clysonymus* and *hortense* is uncertain because, though they are similar both morphologically and in color-pattern, the range of the former in Central America does not extend up to that of *hortense* (Map 22). In view of its advanced morphological features, *hortense* can hardly be a North American relic as is possible for *lineatus*.

Many of the species alleged to have evolved in the Amazon basin have spread over more or less the whole range of the genus. It has already been noted that those species possessing the B-Y-R facies adopt another pattern outside the Amazon basin, but the iridescent blue and yellow species (IB-Y) have retained their characteristic configuration with only minor modifications over their whole range, as in *sarae*



TEXT-FIG. 173. Dendrogram illustrating the evolutionary relationships of *Heliconius*.

wallacei, antiochus and *doris doris*. This pattern may be disruptive and without mimetic significance. The only form of *H. sapho* that occurs beyond the range of the mimetic *H. cydno* is *congener* from the eastern Ecuadorian Andes, which also has the iridescent blue ground color and a pair of forewing yellow bands.

Heliconius doris is one of the more remarkable species, for through dichromatism it effects both the B-Y-R and IB-Y patterns. The forms *doris* and *aristomache* have normal yellow forewing bands but accomplish the iridescent blue effect by having a brilliant blue ray pattern on the hindwing. These two forms are widely distributed over South and Central America respectively. In the Amazon basin there is a dichromatic form *delilae* in which the blue rays are overprinted with a bright red and there is red dennis on the forewing. This produces a good B-Y-R appearance. However, in Central America there is another form, *eratonius,* in which the blue rays are overprinted by red rays of a different type from those of *delilae*. Though it seems that the red rays have evolved independently in the *doris* of Central America, the stimulus is not known. In southern Central and northern South America, *H. doris* is trichromatic, for in addition to the forms with blue or red rays there are forms with green rays which are composed of variable combinations of yellow, green and blue scales. The significance is not known but the pattern of the rays is similar to those of the blue forms. While it is possible that the wing colors in *Heliconius* may be influenced by the larval food plant, in *H. doris* this is not the case, for in Trinidad all three forms have been reared from one brood of eggs laid by a single female and fed on one species of *Passiflora*.

In review, it seems that the existing species of *Heliconius* still portray the phases through which the color-patterns have passed. The figures in parentheses refer to the color plates of Seitz (1913). There are also some excellent color plates in Eltringham (1916).

It is suggested that the earliest *Heliconius* were orange with longitudinal black markings as in *alipherus* (80a), *lybius* (80a), *lineatus* (79f) and *Colaenis iulia* (84b). The evolution of yellow pigment would have led to the design of *natteri* (78f), which with the exposure of spots and bars of ground color in the light areas yields patterns like those of *isabellae* (80d-g), *vibilius* (79e, f), *longarenus* and *charitonius* (79a). Accentuation of the spottedness of the forewing and the richness of the orange of the hindwing

gives the pattern seen in *edias* (79d, e), *hecalasius* (76e), *godmani* and the diversity seen in *numatus, aristionus* and *ethillus* (72-74). Concentration of the forewing yellow into discrete bands, together with reddening of the hindwing, produces the pattern of *himerus* (78a), *hierax* (77d), *hygianus* (79a), *clysonymus* (79b), *hortense* (79c) and *ricini* (79d).

The iridescent blue ground color with discrete yellow forewing bands (the IB-Y pattern of *wallacei* (77d-e), *sarae* (77f, 78a), *leucadius* (77f), *antiochus* (77f), *sapho* (77e)) is considered the penultimate pattern, the most recently evolved being the independently acquired dennis-ray (B-Y-R) characters of *melpomene* (75, 76a-d), *erato* (78a-f), *aoede* (76f) *xanthocles* (77b), *burneyi* (77a), *egerius, elevatus, demeter* (78e) *eanes* (80c) and *tales* (80b).

VI. Summary

From a study of the meso- and meta-pretarsal paronychia, female abdominal processes, spermatheca, signa and protarsi, male genital valves and androconial distribution, alary color-pattern and geographic distribution, the genus *Heliconius* is shown to be composed of forty-six species in thirteen species groups in the two subgenera *Eueides* and *Heliconius*. The geographic variation and polychromatism within these species is described and discussed and a hypothetical evolutionary history is postulated for the genus in conjunction with the palaeogeography of Central and South America.

VII. General References

Eltringham, H.

1916. On specific and mimetic relationships in the genus *Heliconius*. Trans. R. ent. Soc. Lond., 101-148, 117 figs., 2 col. plates.

Emsley, M. G.

1963. A morphological study of imagine Heliconiiae (Lep. Nymphalidae) with a consideration of the evolutionary relationships within the group. Zoologica, N. Y., *48:* 85-130, 153 figs., 17 maps, 1 pl.

1964. The geographical distribution of the color-pattern components of *Heliconius erato* and *Heliconius melpomene* with genetical evidence for the systematic relationships between the two species. Zoologica, N. Y., *49:* 245-286, 15 tabs., 15 figs., 1 map, 2 col. pls.

Lloyd, J. J.

1963. Tectonic history of the south Central-American orogen. *In* Backbone of the Americas, a symposium, ed. Childs, O. E. and Beebe, B. W., Memoir 2, Wisconsin.

Michener, C. D.

1942. A generic revision of the Heliconiinae (Lepidoptera, Nymphalidae). Am. Mus. Novit., No. 1197: 1-8, 17 figs.

Neustetter, H.

1929. Heliconiinae. *In* Lepidopterorum Catalogus (Edit. Strand), pt. 36: 1-136, Berlin.

Seitz, A.

1916. Macrolepidoptera of the world, *5*. The American Rhopalocera. Heliconiinae: 375-399, 593-597, pls. 72-80, (With appendix).

Sheppard, P. M.

1963. Some genetic studies of Müllerian mimics in butterflies of the genus *Heliconius*. Zoologica, N. Y., *48:* 145-154, 2 pls.

Stichel, H., & H. Riffarth

1905. Heliconiidae. Das Tierreich, *22*: 1-290, 50 figs., Berlin.

Turner, J. R. G., C. A. Clark & P. M. Sheppard

1961. Genetics of a difference in the male genitalia of East and West African stocks of *Papilio dardanus* (Lep.). Nature, Lond., *191:* 935-936.

Turner, J. R. G., & J. Crane

1962. The genetics of some polymorphic forms of the butterflies *Heliconius melpomene* Linnaeus and *H. erato* Linnaeus. I, Major genes. Zoologica, N. Y., *47:* 141-152, 1 fig., 1 pl.

Weeks, L. G.

1947. Paleogeography of South America. Bull. Am. Ass. Petr. Geol., *31,* No. 7: 1194-1241, 17 figs.